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ABNORMAL SEXUALITY IN ANIMALS
I. GENOTYPICAL

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IN A review of a field of biological enquiry in which great activity prevails, it is inevitable that much that is ill-understood, debated, disputed, shall be treated in a somewhat arbitrary and even dogmatic manner. It is inevitable too that the reviewer must be found guilty of the faults of misunderstanding, of misinterpretation, and of misused emphasis. Much of great suggestiveness has been omitted since the exigencies of space have made it necessary to prefer just that material which should make the story march easily.

The space at the disposal of the writer does not allow a complete review. The present contribution is therefore limited to the genetics of the subject; the physiological aspects of abnormal sexuality in animals will be reviewed in an early number of the QUARTERLY REVIEW OF BIOLOGY.

SEXUALITY

Sex is the term used to define that differentiation of different parts of an individual, or of the individual itself at different times, or of different individuals, which is associated with the elaboration of physiologically and often morphologically dissimilar gametes. Maleness is the state or quality associated with the elaboration of spermatozoa (or of their physiological equivalents); femaleness is the state or quality associated with the elaboration of ova (or of their physiological equivalents). Sexuality is the state or quality of being distinguished by sex. A male is an individual that exhibits the state or quality of maleness; a female one that exhibits the state or quality of femaleness. If in a group (e.g., a species) it is customary for maleness and femaleness to be exhibited by one and the same individual, coincidently or in succession, the group and the individuals comprising it are monoecious, hermaphrodite, though it follows that in certain cases an individual can at one time be a male and at another a female. If in a group it is not customary for maleness and femaleness to characterize one and the same individual, the group is dioecious, bisexual; the sexes are separate, and every individual within the group throughout its sexual life is either a male or else a female.

Though attempts to classify the sex-dimorphic characters for purposes of discussion have been many, it has to be confessed that as yet no satisfactory classification exists. That this is so is due to the fact that as yet no exact knowledge exists concerning the genetic nature of many of these characters and of their relation to the sex-glands, and until this has been secured any attempt to classify them must be premature. For the present it is enough to hold that the characters which in their combination constitute maleness and femaleness respectively are characters in the genetic sense, being expressions of a genotype that is determined by the nature of the genes brought into the zygote by the conjugating gametes. In the fertilized egg there are none of the characters that distinguish race from race, male from female, that make each individual the first and last of its identical kind; these are expressed as ontogeny proceeds and their expression is modelled, encouraged, embarrassed, to a greater or lesser extent, by the impress of the agencies of the external environment, the outer world, and by the changing conditions within the developing zygote itself, the internal environment, established by the whole of the genotype in action and by the functional activity of the characters as these become differentiated. As a working hypothesis, it can be accepted that sexuality is primarily based upon antecedent determiners within the germ-plasm, upon genes resident in the chromosomes.

In an ever increasing number of instances it can be shown that the phenotypic differences distinguishing male and female are associated with constant differences in the chromosome content of the tissues of the two sexes. This fact is illustrated in the clearest possible manner in the case of *Drosophila melanogaster* which has four pairs of homologous chromosomes. In the somatic cells and immature gametes of the male one of the four pairs is remarkable in that its members are morphologically dissimilar whereas in these tissues of the female the members of this pair are, as is the case in all the other pairs in both male and female, morphologically alike. Since tissues from male and female differ chromosomally only in this respect, these chromosomes are referred to as the sex-chromosomes and the members of the sex-chromosome pair in the female and the

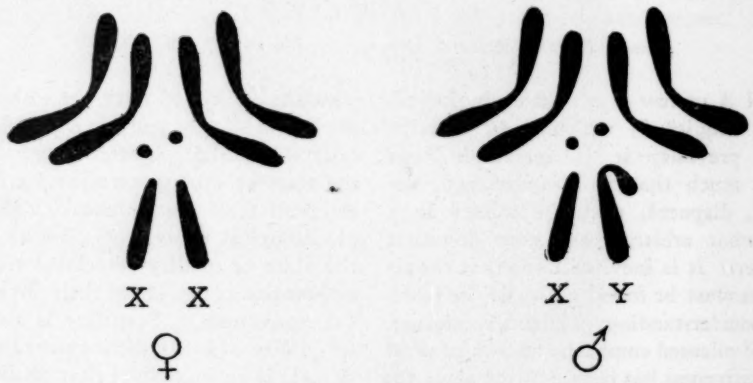


FIG. 1. CONVENTIONAL DIAGRAM OF THE CHROMOSOMES OF *Drosophila melanogaster* (AFTER MORGAN)

one sex-chromosome of the male that is morphologically similar to these are known as the X-chromosomes, whilst the unequal mate of the X in the male is known as the Y-chromosome. In respect of the sex-chromosomes the female is XX, the male is XY.

The situation thus arises that in all the cells of the body of the female and in her immature ova there are four pairs of homologous chromosomes, and of these one pair consists of two X-chromosomes, whereas in all the somatic cells and immature gametes of the male there are four pairs and of these one consists of an X-chromosome in association with a Y-chromosome. Into each ripe gamete there passes one or other member of each pair. All eggs are alike in that each contains an X-chromosome but there will be two kinds of sperm, one containing three autosomes and one X-chromosome, the other three autosomes and a Y-chromosome. When egg and sperm unite in fertilization, into the zygote will be received one member of each pair from the father by way of the sperm and the other member of each pair from the mother by way of the egg, and there will be two forms of zygotes, one that received an X-chromosome by way of the sperm, the other that received a Y-chromosome. The first will have a sex-chromosome constitution that can be symbolized as XX, the chromosome constitution typical of a female, the other a sex-chromosome constitution symbolized as XY, that of a male.

In other cases the chromosome difference between the sexes takes the form of a difference in the number of the sex-chromosomes; for example, there may be in one sex a single X-chromosome, as in the male of many mammals, while in the other there are two. In other groups, e.g., the bee, male differs from female in that one sex is haploid in respect of its chromosome number, possessing but half the number characteristic of the opposite (diploid) sex. It will be seen, as the argument proceeds, that there is considerable difficulty in bringing this type of chromosome difference into line with others, and one is tempted to wonder if all the facts concerning the relation of sex and chromosomes in this group are known.

Our knowledge of the genetics of *Drosophila*, based upon the magnificent and

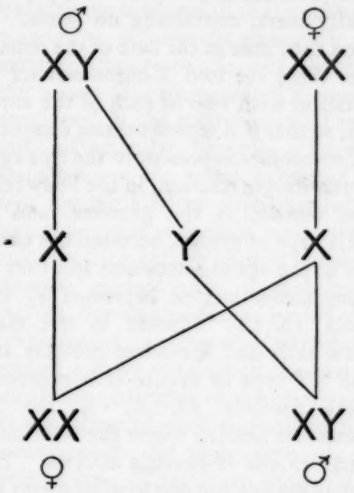


FIG. 2. THE SEX-CHROMOSOME SEX-DETERMINING MECHANISM

inspiring work of Morgan and his associates, is such as to warrant the statements that hereditary characters are the end-results of the action of genes resident in the chromosomes; that in one and the same chromosome is resident a certain orderly company of genes; that each gene has its own particular locus in a particular chromosome; that the genes are arranged in a definite linear order in the chromosome; and that a gene is a certain local area of active chromatin exhibiting a definite

kind of organization capable of undergoing reorganization spontaneously, or maybe under the impress of certain as yet undefined environic stresses, and that it exerts its action and produces its end-results through the medium of the products of its metabolism, substances possibly enzymatic in nature.

The facts of sex-linkage (Morgan, 1914) non-disjunction (Bridges, 1916), and deficiency (Bridges, 1917; Mohr, 1923) are sufficient to warrant the assertion that in *Drosophila* the Y-chromosome is physiologically inert, containing no genes. It follows then that in the case of the female tissues there are two X-chromosomes in association with two of each of the autosomes, so that if A represents one complete set of autosomes as present in the ripe egg, the quantitative relation, in the body cells of the female, in the gametes, and in the XX type of zygote, between the chromatin in the sex-chromosome and that in the autosomes can be expressed by the formula 1X:1A, whereas in the male somatic cells and immature gametes and in the XY type of zygote it is expressed by the formula 1X:2A. In the X-chromosome bearing sperm the relation is 1X:1A, in the Y-bearing 0X:1A. The fact that the egg and one kind of sperm are both, in this respect, 1X:1A and that the other kind of sperm is 0X:1A is of interest in that it shows quite conclusively that gamete and zygote are entirely dissimilar in spite of the fact that each may exhibit a similar X:A ratio. In non-disjunction it is common to get an XY-bearing egg which is, in every way, an egg and in no way is an XY individual, a male. That part of the genotype which is concerned in the morphological aspects of sexuality in the zygote is not liberated until egg has been activated by sperm. As will be seen, the genotype of the gamete has no constant relation to the structure of the gamete for the latter is determined by the kind of organization of the gonad that manufactured it: an ovary elaborates eggs without reference to their genotype and a testis elaborates sperm without reference to their genotype. A gamete 1X:1A in genotype will be an egg if it is the elaborated product of an ovary: a sperm if it is elaborated by a testis.

Since it is established that the genes in the X-chromosomes are different, as judged by the end-results of their action, from those on the autosomes, and that the chromatin organization of any chromosome can exhibit change, it follows that chromatin of the X and of the autosomes is different in its organization and therefore in its physiological activity. Thus the quantitative balance between the X-borne and the autosomal-borne genes differs in male and female tissues and the physiological states established by the interaction of genes in male and female zygotes respectively will likewise be dissimilar.

It is not necessary, it is probably entirely incorrect, though it is undoubtedly convenient, to postulate male-determining and female-determining genes, especially concerned in determining sexuality. Maleness in *Drosophila* is that physiological state or quality established in a zygote as the result of the action and interaction of all the genes in a genotype that may be symbolized as 1X:2A. In the beginning, maleness in the zygote is a certain kind of internal environment, a certain metabolic level: femaleness is another, and in one or the other organogeny and ontogeny proceed. In the XX type of individual an internal environment of femaleness becomes expressed and the structures that pertain to the sexual organization will pursue their differentiation under the direction of their own genotype, in the presence of the physiological stimuli exerted by other differentiating and dif-

ferentiated tissues, and in an external environment which may condition this differentiation. On the other hand, in the XY zygote an initial internal environment of maleness becomes established and the differentiation of the sexual organization during ontogeny will be such as will yield a typical phenotypic male.

An individual in the case of *Drosophila* is a phenotypic male (1) because in the beginning it was a genotypic male (XY); (2) because in this XY zygote the relation between the X-borne and the autosomal-borne genes (the ratio between their number or their algebraic sum, as suggested by Schrader and Sturtevant (1923) as an explanation of the facts of sexuality in those cases in which one sex is haploid, the other diploid) was such that an internal environment of maleness became established; (3) because in this internal environment the structures concerned in the sexual organization, being XY in chromosome constitution, developed, and in developing flourished; and (4) because the impress of the external environment did not or could not affect the developing zygote in such a way as to override the effects of the gene mechanism and to modify the internal environment based thereupon so that it became physiologically equivalent to that type of internal environment that is normally associated with the genotype symbolized as XX. For similar reasons the genotypic female becomes a phenotypic female. *Propter secretiones internas totas mulier est quod est*, a female is a female by the totality of her internal secretions, remains true only if it be granted that the phrase "internal" secretions shall include the metabolic products of her initial genotype.

In the vertebrates the initial sexuality, which is but the direct expression of genetic action, is strongly reinforced when the components of the endocrine system become differentiated. The results of experimental gonadectomy and of the implantation of gonadic tissues have clearly demonstrated the intimate relation between the type and degree of sexual differentiation and the functional activity and histological organization of the gonads (Steinach, 1912; Sand, 1921, 1923; Moore, 1921; Lipschutz, 1924). They have shown conclusively that for the complete differentiation and maintenance of the sexual phenotype active functional gonadic tissue is essential, that a male possessing testes, because the embryonic gonads assumed the testicular organization for the reason that they were XY tissues and developed in the initial internal environment of maleness, becomes a phenotypic male because the testes exhibited a certain specific kind of physiological activity, elaborated a specific male "sex-hormone" which greatly reinforced the initial internal environment of maleness and exerted, during the critical period of their development, a directing stimulus that evoked a ready response on the part of the remaining structures of the sex-equipment so that these pursued their differentiation according to the male type of sexual architecture. They have shown that an individual becomes a phenotypic female because it possessed functionally active ovaries at the time when the rest of the structures of the sex-equipment underwent differentiation. When it has been shown how it is that she comes to possess ovaries, there remains no difficulty in showing how it is that she becomes equipped as an efficiently functional female.

It is not to be denied that for the efficient differentiation and maintenance of the sexual equipment the activity of other members of the endocrine chain is essential (Bullock and Sequira, 1905; Glynn, 1911–12; Berner, 1923; *et alia*), but for the pres-

ent it is reasonable to assume that the rôle of such glands as the adrenal, the pituitary, the thyroid, in sexual differentiation, is relatively unimportant when compared to that of the differentiated gonad.

Reviewing that which has been written above, the sexual characterization in the mammal can be summarized, for purposes of discussion, as follows. It is to be noted that in the case of the bird the female is the digametic sex (XY) and the male monogametic (XX). In the vertebrate groups that have been examined the sex-chromosome constitution is as that which obtains in the case of *Drosophila*. (Painter, 1921–1924; Bachuber, 1916; Stevens, 1911; Wodsedalek, 1913, 1914, 1916, 1920; Winiwarter and Sainmont; 1909; Allen, 1918; Malone, 1918; Zeleny and Faust, 1915; Parkes, 1923; Yocum, 1915, 1917). (See table 1.)

Reasons for holding that the gonads, in certain vertebrate groups, e.g., birds, do not function as endocrine glands, elaborating specific sex hormones, will be considered later.

In the case of insects (Oudemans, 1899; Kellogg, 1904; Prell, 1915; Kopeć, 1911, 1922; Meisenheimer, 1909; Hegner, 1914) it has been established by experimental

TABLE 1

	MALE	FEMALE
1. *Primary genotypic sexual characters*		
The sexual genotype symbolized as	XO or XY	XX
an internal environment symbolized as	1X:2A	1X:1A
in which ontogeny proceeds and the phenotype is assumed		
Secondary genotypic sexual characters are developed. These include:	Such sexual differences as are not secondary gonadic (many of them are epigamic, i.e., concerned only indirectly with, but contributory to, fertilization, playing their part in courtship and the care of the young)	
2. *Primary gonadic characters*		
The *gonads* become differentiated	Testes	Ovaries
The '*sex-hormone*' is liberated and the following become differentiated	Male sex-hormone	Female sex-hormone
Secondary gonadic characters		
(1) The accessory sexual apparatus (Müllerian and Wolffian ducts)	Wolffian duct derivatives flourish	Müllerian duct derivatives flourish.
	Müllerian duct derivatives cease their development	Wolffian duct derivatives cease their development.
(2) The external genitalia		
Urogenital sinus	Scrotum	Vulva
Phallus	Penis	Clitoris
(3) Certain of the epigamic characters which for their expression depend upon the stimulus of the differentiated gonad, and becoming expressed at different times as they reach the stage of their development when they can respond	e.g., regional distribution of hair, mammary glands, voice.	

gonadectomy and the implantation of gonadic tissues that no part of the control of sexual differentiation is, in these forms, relegated to the gonad. All the sexual characters of the insect are secondary genotypic and owe nothing in their differentiation to the physiological activity of the differentiated gonad. The differentiation of a cell is pursued under the control of its own genotype.

Finkler (1923) has carried out some vastly interesting experiments with various orthoptera (*Hydrophilus*, *Dysticus*, *Notonecta*, *Dixippus*, *Tenebrio*, *Vanessa*). He transplanted male heads on to female bodies and *vice versa* and observed the effect of this upon sexual behaviour. In the case of *Hydrophilus*, three operations were entirely successful, complete healing occurring in about seventeen days when all movements were properly coordinated, and feeding and defecation were normal. A female with a male head behaved sexually as a male towards females and a male with a female head as a female, but was regarded by normal males as a male. In certain instances the body took on the coloration of the sex to which the transplanted head belonged. Blunck and Speyer (1924), repeating this work, failed to confirm Finkler's findings.

Abnormal Sexuality

1. intersexuality

If in an individual of a group in which bisexuality is customary, maleness and femaleness are exhibited coincidently or in succession and to any degree, that individual is an intersexual form. It is an intersex either in time or in space. Intersexuality is the state or quality exhibited by an individual of a normally dioecious group in which both maleness and femaleness are to be distinguished in varying degree and/or at different times. Hermaphroditism is the expression of a sexuality normal to a particular group: intersexuality, transient or permanent, an expression of sexual abnormality in a particular group or individual. Hermaphroditism and intersexuality are the same expression of the self-same mechanism but whereas intersexuality is perfect or imperfect hermaphroditism in a non-hermaphroditic group or individual, hermaphroditism is perfect intersexuality in a group or individual in which such a state or quality is a customary feature of the normal life history.

From what is known of the mechanisms of sex-determination and sexual differentiation it can be anticipated that intersexuality in a normally dioecious group will follow upon (1) disharmony in the sexual genotype of the body as a whole or of local parts, and (2) profound alteration of the internal environment during critical stages of development.

A. Disharmony in the distribution of the genotype

1. Gynandromorphism. *(a) Gynandromorphism in Drosophila melanogaster.* A gynandromorph is an individual of a bisexual species which exhibits a mosaic of male and female sexual characters: it is a sex mosaic in space. In the case of *Drosophila melanogaster* about 1 in every 2,000 individuals exhibits this condition of gynandromorphism. Most of these are bilateral gynandromorphs, exhibiting the complete male characterization on one side of the antero-posterior mid-line of the body, the complete female characterization on the other, with a sharply demarcated line of junction of the two kinds of tissue. Since the male body is normally smaller than that of the female the gynandromorph's body is bent towards the male half. Usually in these cases there is an ovary on the female side, a

testis on the male, but this is not always the case, nor would it be expected that it should be, for, as Huettner (1922) has shown, the gonads are not formed from a single nucleus but from several nuclei which give rise to the primordial germ cells and so it is not inevitable that both gonads should be histologically and cytologically similar. Commonly, however, they are two ovaries or two testes in a bilateral gynandromorph. In other cases of gynandromorphism one quarter of the body is male in its sexual characterization, three quarters female: in still others less than a quarter is male and more rarely the head is female whilst the rest of the body and abdomen are male.

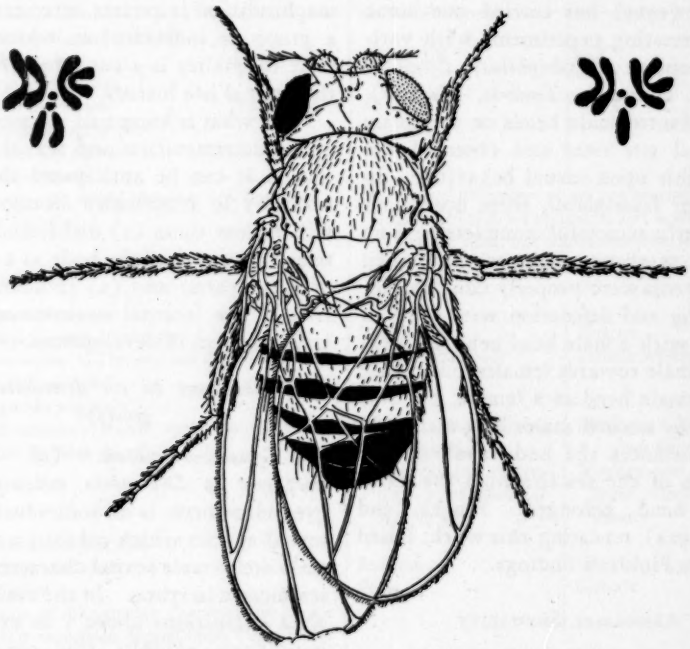


FIG. 3. A GYNANDROMORPH (FROM MORGAN, BRIDGES AND STURTEVANT)

Morgan and Bridges (1919) have described many of these sexually abnormal forms in great detail and have shown that if in the mating that produces the gynandromorphic forms sex-linked characters are involved, and if the sex-linked characterizations of the two parents are dissimilar, then the sex-linked characters of the male parts are those exhibited by the father or those exhibited by the mother whereas the sex-linked character of the female parts are a combination of the sex-linked characters of both parents, and that, in respect of the autosomal (non sex-linked) characters, male and female parts are alike. The example depicted above is a bilateral gynandromorph, the left side exhibiting a typical female characterization, the right a typical male. The left side presents the dominant sex-linked character, Notch, (the mother was

Notch), and the right exhibits the recessive sex-linked characters scute, broadwing, echinus eye, ruby eye, tan bodycolor, and forked bristles (the father had these characters).

These facts point to the conclusion that gynandromorphism in such a case as this results from aberration in the distribution of the X-chromosomes. If it is assumed that the gynandromorph is in its beginning an XX-zygote, a genotypic female, and that at some stage during the early cleavage divisions of the fertilized egg, a daughter X-chromosome fails to enter one of the daughter cells, this cell will then contain one X instead of two, i.e., will have the chromosome content of a genotypic male. Since one X is derived from the paternal contribution of nuclear material and the other from the maternal and since, if the parents were dissimilar in their sex-linked characterization these two X-chromosomes will be dissimilar in their gene content, it follows that the characterization based upon genes in either of them can be markedly different from that based upon the genes in both. In the example described above the mother (XX) carries in each of her X-chromosomes (shaded) the gene for the dominant sex-linked mutant character Notch. The father (XY) carries in his single X-chromosome (unshaded) the genes for the recessive sex-linked characters scute, broad, echinus, ruby, tan, and forked. The F_1 female zygote will receive one X-chromosome from each parent. She will exhibit the dominant character Notch and not scute, not broad, not echinus, not ruby, not tan, and not forked—the dominants of both parents. If during the first cleavage division of this zygote the maternal X-chromosome fails to enter a daughter cell the paternal X alone will be present therein and the tissues that develop from this daughter cell will be 1X:2A (male) in constitution and cannot be Notch but will exhibit, if they belong to the appropriate parts, the recessive sex-linked characters of the father. Had it been the paternal X that had been eliminated, the male side of the gynandromorph would have exhibited the sex-linked character of the mother, Notch.

In the absence of further aberrations in chromosome distribution all the cells that have their origin in the XX daughter cell will have the 1X:1A type of chromosome relationship: all the cells that arise from the single X-containing daughter cell will have the 1X:2A type, and the sex-linked characters of the tissues formed by these latter will exhibit, if they pertain to parts that do exhibit sex-linked characters, those of the parent from whom their X-chromosome was derived. If this is the case, then a gynandromorph of a grade that is compatible with fertility, i.e., one in which the abdomen and genitalia are female, should prove to be heterozygous in respect of her sex-linked characterization. This is the case. On the other hand, if the abdomen and genitalia are of the male type of architecture, the individual should be sterile, since in these parts the sex-chromosome constitution is XO and it is known from Bridge's nondisjunctional work (1916, 1919) that the XO male in *Drosophila* is sterile. This is also the case.

If the elimination of the X-chromosome occurs at the first cleavage division of the zygote, the gynandromorphism is bilateral: if it occurs at the second, one quarter of the body will be male in its characterization. Elimination may occur at any stage of ontogeny and the later it occurs the smaller will be the area that exhibits male type characterization. But however large or small this area may be, it will pursue its development under the direction of its own genotypic constitution

(except in the case of vermilion eye, Sturtevant, 1920) and its differentiation is not influenced by the physiological activity of the gonads.

It is to be noted that these mosaic formations are not limited to the sexual phenotype: they are commonly found involving the general phenotype in hybrids. tion of an X-chromosome at a cleavage division, but one specimen was a mosaic both for sexual characters and for mutant characters in chromosome III. Analysis of this case showed that in its production two spermatozoa were involved and that it was the result either of the synchronous fertilization of a double nucleus egg by

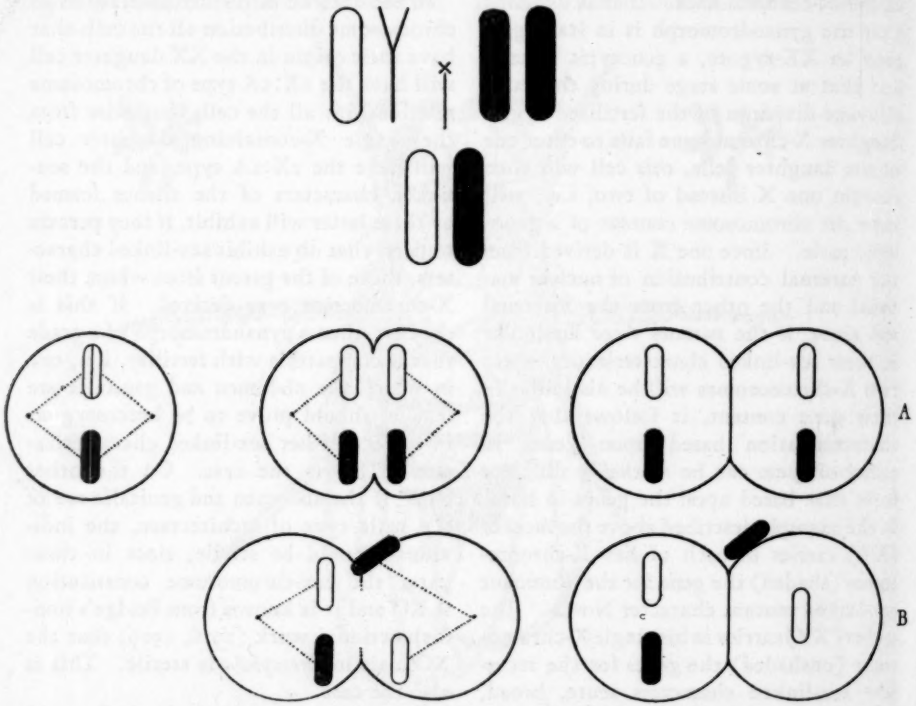


FIG. 4. GYNANDROMORPHISM FOLLOWING THE ELIMINATION OF AN X-CHROMOSOME
A, normal distribution of chromosomes; *B*, abnormal distribution of chromosomes

Gynandromorphism results only from such aberrances in the distribution of nuclear chromatin that lead to a sufficient disturbance in the X:A ratio.

(*b*) *Gynandromorphism in D. simulans.* Gynandromorphs have occurred fairly commonly in *Drosophila simulans* (Sturtevant, 1921). Most of these are to be interpreted as the result of the elimina-

two sperm or to polyspermy in a single nucleus egg.

(*c*) *Gynandromorphism in the bee.* There are certain facts relating to sex-determination in the bee that are unique. The queen is diploid and this double set of chromosomes is reduced to the haploid number in the ripe egg after two polar bodies have been extruded. If the egg is

fertilized, it gives rise to a female (queen or worker) but if it is not fertilized it yields a male (drone). The male has the haploid number of chromosomes but whether sex-determination is the result of the action of a chromosome mechanism has not yet been determined. It is necessary to assume that the sex-determining mechanism in the bee and similar forms is essentially different from that which obtains in the case of *Drosophila*. It is remarkable that the male is a haploid individual and that the diploid individual is not a male for the ratios among the sex-determining genes are not different in the two cases. The case of the bee is so unique that it merits further investigation. Disagreement with a system that obtains so widely, and an interpretation that is so satisfactory must always be a stimulus for further investigation and not merely a missile for a critic's hand.

In the bee the mother transmits her characters directly to her sons as is the case in the typical sex-linked mode of inheritance in *Drosophila*. But the reason for this is that the male develops from an egg that has received no paternal chromatin. There is certain reliable evidence which strongly suggests that there is a chromosome in the bee that is equivalent to the X-chromosome of *Drosophila*. Hybrid queens produce two kinds of males and two only, which fact indicates that a single factorial difference exists and that the allelomorphs are carried by a pair of chromosomes, not necessarily sex chromosomes, but possibly so. The elimination hypothesis which seeks to explain gynandromorphism in the bee demands that the elimination must involve a sex-chromosome and that this must also be the one that carries the genes concerned in the production of racial characters.

In the sixties of the nineteenth century Eugster kept at Constance a hive of bees which consisted of hybrids out of a yellow Italian queen by darker German drones and which regularly produced a large number of gynandromorphs. This regularity in the production of abnormal forms points to the conclusion that the abnormality is genetic and not merely accidental or due to specific environmental impresses. When the Italian queen died Eugster replaced her with a hybrid queen and she in turn produced gynandromorphs. V. Siebold first examined these specimens in 1864, and attempted to account for these gynandromorphs by assuming that an insufficient number of sperm had penetrated the egg so that parts of it lacked sufficient quantities of the male contribution. It is to be noted that Nachtsheim (1913) has since shown that polyspermy is customary, but this interpretation does not explain all the phenomena encountered. They have been re-examined by Boveri (1915) and Mehling (1915). The specimens ranged from an almost perfect male to an almost perfect female. Since they were hybrids, it was possible to tell from their characterizations whether the tissues concerned contained paternal, maternal, or both paternal and maternal nuclear material. Boveri concluded that all the male parts were purely Italian in their characterization, whereas the female parts were definitely hybrid, exhibiting the characters of both races. If this were so, it follows that in the tissues of the male parts there was no nuclear material brought into the zygote by the sperm but only that contributed by the ovum.

In order to explain this, Boveri suggested that the sperm did not reach the egg nucleus before the latter had begun to segment and so fused, not with the whole egg nucleus, but with one of the daughter nuclei (partial fertilization). Two blastomeres would thus result, one containing

only the maternal nucleus whilst the other would include both maternal and paternal nuclear material. It is established that in the case of the bee, if the egg which contains the haploid number of chromosomes is fertilized it becomes a female: if it is not fertilized, it becomes a male. The male is haploid, the female diploid in respect of its chromosome content. It follows then, that in the case of the late fertilized egg, the blastomere that contains both maternal and paternal nuclear material is diploid, i.e., female, the blastomere that is not fertilized remains haploid, i.e., male.

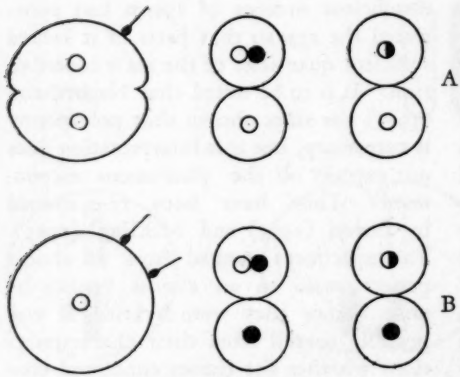


FIG. 5. INTERPRETATIONS OF GYNANDROMORPHISM

A, partial fertilization of Boveri; *B*, polyspermy of Morgan.

Morgan has suggested that the same results would follow if two sperms should enter one and the same egg, but only one of them unite with the egg nucleus (polyspermy). Doncaster (1914) has pointed out that, as seen in his *Abraxas* work, this gynandromorphism could be explained as the result of the synchronous fertilization of two egg nuclei.

If the gynandromorphism is the result of partial fertilization, then the male side should exhibit the characters of the mother's race (Italian) because its haploid chromosomes came directly from the Italian mother egg, whilst the female side should exhibit the dominant characters of both Italian and German races. If, on the other hand, the condition results from polyspermy, then the male parts should exhibit the characters of the father's race (German). Boveri, examining the preserved specimens (47 years in alcohol), reached the conclusion that the male parts were Italian in their characterization. If this is the case, then Boveri's hypothesis is to be preferred to that of Morgan.

But Engelhardt (1914) has described some fresh gynandromorphic specimens out of an Italian mother by a father very similar indeed to that of the males of the Eugster hive. The male parts presented the paternal characterization. This supports Morgan's interpretation.

Morgan and Bridges are of the opinion that the case of Eugster's bees can equally readily be explained by assuming that, as in the case of the *Drosophila* gynandromorphs, there is an accidental elimination of a sex-chromosome during cleavage. The bees concerned were *A. ligustica* (Italian), and *A. mellifica* (German). If it is assumed that one of the postulated sex-chromosomes of the hybrid carried the gene-complex for the *ligustica* characterization, the other the *mellifica*, and if the *mellifica* chromosome is eliminated, then a cell containing only the *ligustica* chromosome would result and all parts descending from that cell would be male (haploid) and *ligustica*. This is the result observed by Boveri. If the *ligustica* chromosome is eliminated the result is male tissue and *mellifica* characterization. This is the result observed by Engelhardt. This interpretation accommodates both Boveri's and Engelhardt's observations whereas Boveri's partial fertilization and

Morgan's polyspermy each only explains one. If *mellifica* is dominant to *ligustica*, then the female parts will be *mellifica* as described by Boveri. But Newell (1914) who crossed Italian queen and gray Carniolan drone got yellow daughters, showing that the yellow was dominant. In this case both sides would be alike if in the male parts the *mellifica* chromosome had been eliminated, and this may have been the reason for v. Siebold's omission to mention in connection with the fresh Eugster specimens that the parts were which the chromosome distribution is abnormal, the end-result will be bilateral, quartal, or some other grade of sex mosaic.

For further instances in other forms see Sandhouse (1923), Wheeler (1910), and Nachtsheim (1923).

(d) Gynandromorphism in the silkworm. Among the Lepidoptera over 1,000 cases have been described (see Wenke, 1906). They can all be explained on the assumption that there has been elimination of an X-chromosome in the XX (male) zygote. Toyama (1906) has described

Egg		*Sperm*	
(WX)	×	(wX)	This half will develop, will be male (XX) and zebra (Ww)
(WX)			This half will develop, will be female and zebra.
Y	×	(wX)	This half will develop, will be female and white
Y			This half will not develop.

Morgan's polyspermy interpretation.

(WX)	×	(wX)	This half will develop, will be male and zebra.
—		(wX)	This half will develop, will be female and white.
Y	×	(wX)	This half will develop, will be female and white.
—		(wX)	This half will develop, will be female and white.

Morgan's elimination interpretation.

(WX) (wX)	The zygote.
(WX) (wX)	This cell and the tissues arising therefrom will be male and zebra.
or (WX) (wX)	This cell and the tissues arising therefrom will be female and zebra if one X is eliminated, white if the other.
(WX)Y	The zygote
(WX)Y	This cell and the tissues arising therefrom will be female and zebra.
Y	This cell will not develop.

different in colour. It is not improbable that when Boveri examined his material the specimens were too old to give reliable pictures of color differences. Whichever interpretation is correct, and there is no reason to assume that all instances of gynandromorphism result from exactly the same kind of fault, it is certain that in all cases the underlying cause of gynandromorphism is an abnormal distribution of nuclear material; it is the mechanism of distribution that is at fault. According to the stages of embryonic development at two cases in the silkworm moth (*Bombyx mori*). The mother belonged to a race in which the caterpillar is zebra patterned and the father was of a race in which the caterpillar is uncolored white. Zebra is dominant to white, and these characters were regarded as being sex-linked. In the one case the left female side was zebra, the right male was white.

Boveri's partial fertilization interpretation. The female is XY in the silkworm. She lays two sorts of eggs, the X-bearing and the Y-bearing. Either of these is fer-

tilized by an X-bearing sperm. Let W = the gene for the zebra pattern, w that for white, and let the brackets represent the fact that the gene is resident upon the X-chromosome included therein.

None of these interpretations accommodate the facts of the case. Fortunately Doncaster (1914) had described binucleated eggs in *Abraxas*, each nucleus having given off polar bodies and each having been independently fertilized. Morgan, appealing to this fact, points out that if the zebra mother was heterozygous for this character one nucleus could contain an X-chromosome and an autosome with the gene for white, whilst the other could contain a Y-chromosome and an autosome with some with the gene for zebra. Two sperms of the father carry the X and the autosomal gene for white. Each fertilizing a nucleus would give rise to a male side XX white: white and a female side XY zebra:white. This seems to be the most reasonable interpretation: it demands, as is seen, that the characters zebra and white shall not be sex-linked.

Doncaster's binucleated egg interpretation (Morgan)

Ww XY egg.

WY × wX = Ww XY female, zebra

wX × wX = ww XX male, white

(*e*) *Gynandromorphism in Abraxas.* The characters *grossulariata* and *lacticolor* are typical sex-linked characters. *Lacticolor* male × *grossulariata* female gives *grossulariata* males and *lacticolor* females. Doncaster (1914) found that one mating produced twenty-four *lacticolor* females, no *grossulariata* males, and one gynandromorph, *lacticolor* with the right side of the body male and the left imperfectly developed more like that of the female. The internal genitalia were, as far as was known, imperfectly developed male organs.

The absence of males was associated with an unusual chromosome content in this family (55) for all fertilized eggs lacked a chromosome, the single X passing out into the polar bodies in most cases.

Morgan explains this case as follows.

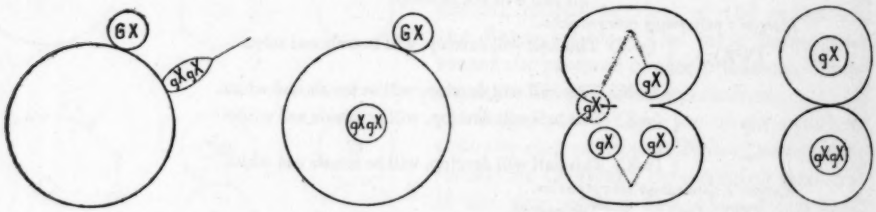


FIG. 6. MORGAN'S INTERPRETATION OF DONCASTER'S CASE

G, gene for *grossulariata*; *g*, gene for *lacticolor*

The egg either contains no X-chromosome and therefore no gene for *grossulariata* or else it does contain this X and the gene for *grossulariata*. The male in *Abraxas* is XX. A sperm carrying the *lacticolor* gene-bearing X-chromosome fertilizing the no-X-egg will yield an XY zygote, a female and *lacticolor*. A similar sperm fertilizing an X-bearing egg will yield an XX zygote, a male, and *grossulariata*. Only through the fertilization of a no-X egg by a two-X-bearing sperm could a *lacticolor* male arise. Such a sperm could result from non-disjunction. If the zygote which developed into this gynandromorph was such an XX male (both X's having been derived from the father) then the

gynandromorphism would be due to the elimination of one of these X's at some early division.

Doncaster's second case is one that readily lends itself to interpretation as an instance of chromosome elimination. *Lacticolor* male × *grossulariata* female gave eleven *grossulariata* males, eleven *lacticolor* females, and one gynandromorph, the anterior parts of which were male and the posterior parts female. The zygote would be an XX individual, one X bearing the gene for *grossulariata*, the other the gene for *lacticolor*. Elimination of a paternal *lacticolor* X-chromosome would give a *grossulariata* male anterior region (XX) and a *grossulariata* posterior region (maternal X).

(*f*) *Gynandromorphism in Arthropoda, Crustacea, Mollusca, and Echinoderma.* The frequency with which gynandromorphism is recognized in different groups varies with the interest taken by the collector or experimentalist in these groups and with the degree of sex dimorphism that is exhibited. In many forms male and female are very similar in their external characters and in these gynandromorphism will not be detected and in many of the forms in which an occasional instance of gynandromorphism is reported, insufficient is known of the mechanism which in these cases determines sex and models sexual differentiation to allow anything more than a very speculative interpretation being made. It is probable that many cases cited in this connection are not gynandromorphs but are instances of serial intersexuality.

For examples see Kulczynski (1885), Falconer (1910), Hull (1918), Hill (1917), Kuttner (1909), Ashworth (1913), Pelseneer (1920), Nichols (1734), Cuénot (1898), Délage (1902), Herlant (1918).

(*g*) *Gynandromorphism in birds.* Since gynandromorphism is the result of an abnormal functioning of a mechanism it cannot be the normal characterization of a group. It can only affect those tissues the cells of which pursue their differentiations independently of all others. It is, therefore, impossible to find a gynandromorph in those groups in which the control of the processes of sexual differentiation has been completely relegated to some special organ or tissue; it cannot occur in the mammal if in this group sexual differentiation is mainly pursued under the directing stimulus of a sex-hormone elaborated by the differentiated gonad. If in a group, undoubted, and otherwise inexplicable, cases of gynandromorphism are found, then in that group the internal secretions of the gonad do not constitute the sole controlling forces in sexual differentiation and the cells of different parts can pursue their differentiation under the direction of their own genotype.

Gynandromorphism has been recorded in birds. Poll (1909) described a true bilateral bullfinch; Weber (1890) a finch (and refers to two other cases described by Cabanis, 1874); and Bond (1913) a pheasant. In the finches the right side of the body was male and the gonad a testis, the left female, and the gonad an ovary. In Bond's pheasant the left side of the body was male, the right female, and the gonads were ovotestes. The individual tail feathers had one half of the vane with male markings, the other half with female. Macklin (1923) describes a fowl (breed not stated) which had the plumage characterization of a hen with neck-feathering suggestive of that of the male and with tail sickles rather longer than those of the normal hen. (It will be shown later that this tail characterization is associated with the synchronous presence of both ovarian and testicular tissues in experimental birds, either male

or female, and that it is the normal condition in the Campine henny-feathered cock). The comb and right wattles were as those of a cock, and the bird exhibited male behavior, attempting copulation with hens with apparent success. It was not known to crow and it did not fight with cocks. It was known to be laying, but since it was suspected of laying small eggs it was killed. When it was being prepared for the table it was noticed that the right side of the body was distinctly larger than the left and that there was a testis on the right and on the left an ovary (which really was an ovotestis) and an oviduct. The histological examination showed that it could have laid and that there were normal looking spermatozoa and a testis of normal appearance. Every bone on the right side was larger than the corresponding bone on the left, these latter being 66 per cent as heavy and 85 per cent as long.

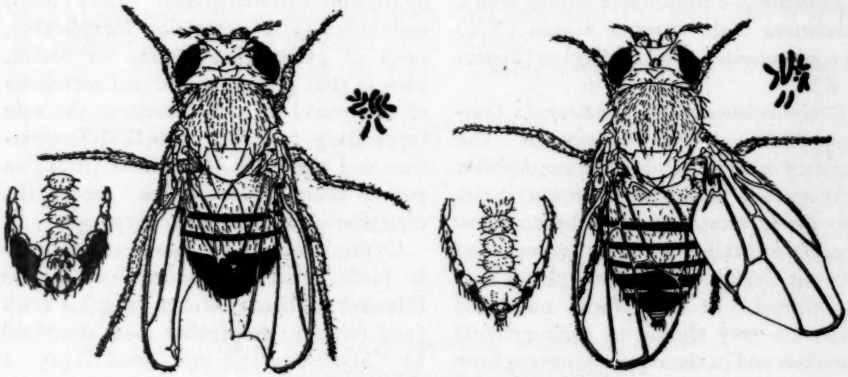


FIG. 7A FIG. 7B

FIG. 7A. MALE TYPE INTERSEX (2X:3A-IV) (FROM MORGAN, BRIDGES AND STURTEVANT)
FIG. 7B. FEMALE TYPE INTERSEX (2X:3A) (FROM MORGAN, BRIDGES AND STURTEVANT)

These cases can best be interpreted as gynandromorphs in a group in which the male is monogametic (XX) and in which the control of the processes of sexual differentiation is not absolutely centered in the gonads. In a male zygote one X-chromosome was eliminated at the first cleavage division of the fertilized egg, or according to the grade of femaleness in the characterization, later at some division of a cell in those areas which are to be involved in the sexual characterization. Evidence in support of the hypothesis that aberration in the distribution of the sex-chromosomes can occur in the somatic cells is to be obtained from a study of the abnormalities in the distribution of sex-linked plumage color characters. Serebrovsky (1925) explains the occurrence of black feathers in a barred silver plumage by postulating that in the cells in which these feathers have their origin, the sex-chromosome, in which the sex-linked factors for barring and for silver are resident, is lost during its transference from mother to daughter cells. The question of the presence of ovotestes in these cases will be discussed later.

2. Balanced intersexuality in Drosophila melanogaster. The 2X:3A (−IV) male and the 2X:3A female intersexes. In an experiment made by Bridges (1921) to deter-

mine the locus of a new second chromosome recessive mutant "brown" by means of a back-cross to plexus and speck, one culture produced 96 females, 9 males and about 80 individuals which were abnormal in their sexual characterization. These intersexes were large bodied, coarse bristled flies with large roughish eyes and scolloped wing margins. The intersexes showed a bimodal variation, one group more closely approaching the female in the abdomen and genitalia was predominantly male. Sex-combs were always present. The gonads were typically rudimentary testes though in a few cases the testes were well developed and contained bundles of sperm.

Moreover, instead of getting but two classes of offspring among the progeny of the back-cross as would be expected, three classes appeared, plexus speck, plexus brown, and brown speck. This unex-

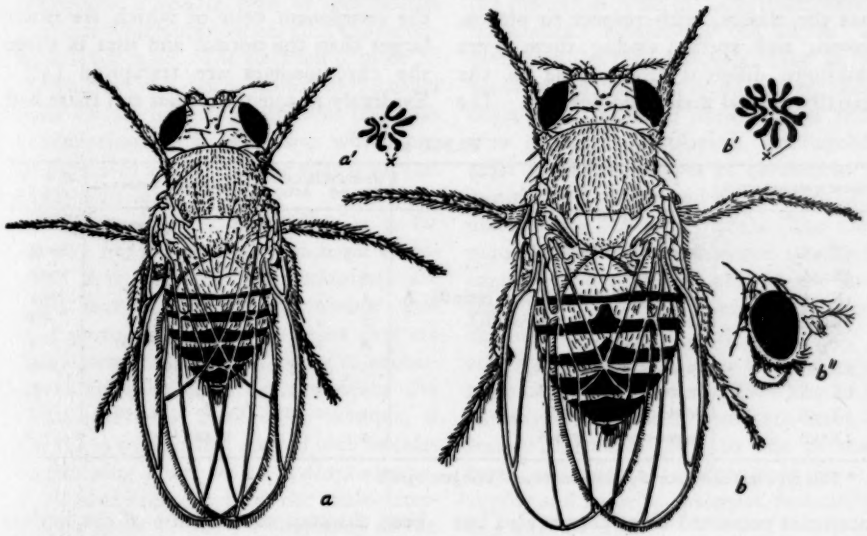


FIG. 8. *a*, NORMAL FEMALE, *b*, TRIPLOID (3N) FEMALE. *b''*, THE LARGE ROUGH EYE (FROM MORGAN, BRIDGES AND STURTEVANT)

characterization, the other the male. All were sterile. In the female type the genitalia were predominantly or completely female, the abdomen was very much as that of the normal female: spermathecae were present. The gonads were typically rudimentary ovaries: in many cases the ovarian tissue had a bud of testicular tissue, in others one gonad was a rudimentary testis, the other a rudimentary ovary. Sex-combs were usually present. In the male type, the characterization of

pected result can only be explained on the understanding that the mothers had three instead of two chromosome II, one carrying plexus brown, one plexus speck, and one brown speck. From their father each had received a chromosome II carrying plexus, brown, and speck, and from the mother they had received one of the three kinds of chromosome-II mentioned. She had two genes for each of the recessive characters, plexus, brown, and speck, and one for each of the alternative dominants.

Further tests showed that the mothers were also triploid in respect of chromosomes I and III whilst chromosome IV was present either in the duplex or triplex state. It was noticed that these 3N (where N = the haploid chromosome number) mothers could be distinguished from the ordinary normal female by their large size, coarse bristles, and rough eyes. That the intersexes were themselves triploid and not diploid with respect to chromosome II was shown by the fact that the classes, with respect to plexus, brown, and speck, among them were strikingly different from those in the sexually normal males and females. The intersexes presented three classes also but these were plexus, speck, and brown respectively.

It was readily possible to put this explanation of triploidy to the test of cytological examination and it was found that all the intersexes carried two X-chromosomes, three of each chromosomes II and III. Certain of them carried a Y-chromosome and some of them had three IV's, others two. It was thought at first the triplo-IV's were the male type, the diplo-IV's the female type of intersex, but further investigation has shown that this is not so; the triplo-IV's are the female intersexes, the diplo-IV's the male. It is to be noted that the infecund female type of intersex differs from her very fecund mother in that she is 2X:3A whereas the mother is 3X:3A, and that in these intersexes the addition of a fourth chromosome makes all the difference between a male type and a female type.

For the production of these intersexes polyploidy must have occurred in earlier generations. Bridges has shown that in certain cases ordinary diploid females possess ovaries in which there are areas the component cells of which are much larger than the normal and that in these the chromosomes are tetraploid (4N). Evidently in some oogonial cell there had been chromosome division of the nucleus so that all mature eggs would be diploid. The same process could occur in spermatogenesis. Should such a diploid gamete fuse with a normal haploid gamete from the mother parent it would give rise to a 3N zygote.

TABLE 2

CHROMOSOME RELATION	SEX TYPES	NUMERICAL RATIO X (100) A(80)	SEX INDEX	INTERVAL	X = −6 A = +2
				per cent	
3X:2A	Super-female (triplo-X)	1.5 : 1	1.88	50	−14
4X:4A	4N female	1 : 1	1.25		−20
3X:3A	3N female (normal since ratio X : A	1 : 1	1.25		−12
2X:2A	2N female is same in all).	1 : 1	1.25		−8
1X:1A*	1N female	1 : 1	1.25	50	−4
2X:3A	Intersex (female type)	1 : 1.5	0.83		−6
2X:3A (−IV)	Intersex (male type)	1 : 1.5	0.83	33	−6
1X:2A	Male (normal)	1 : 2	0.63	50	−2
1X:3A	Super-male (triplo-A)	1 : 3	0.42		−0

* This type has only recently been described (Bridges, 1926).

The following represents the series of sex types in *Drosophila melanogaster*. If the efficiency of the female determining genes (X-borne) is represented as 100 and that of the male determining gene-complex in the autosome as 80, a series of sex-indices can be made. (See table 2).

A review of these facts supports the contention that the initial sexuality of

the zygote is determined by the interaction of the genes resident in the chromosomes, sex-chromosomes, and autosomes alike. The addition of more autosomal chromatin (= autosomal-borne genes) to the usual female 2X:2A balance so disturbs this that the relationship is now that which can be expressed as 2X:3A and results in the establishment of a physiological state in which male type characters develop, i.e., the addition transforms a female type of metabolism into one which approaches that characteristic of the male. The addition of more X-chromatin (= X-borne genes) to the usual male 1X:2A balance so disturbs this that the relationship is now that which can be expressed as 2X:2A, one that is typical of the female.

There can be no doubt that it is far simpler for purposes of discussion to assume that in the X-chromosomes are genes that are "female-determining" and that on the autosomes are genes that are "male-determining" and that the sexuality of the zygotes is determined by the balance between these. For example, if F is taken to represent a set of such female-determining genes on an X-chromosome, if M indicates a set of the male-determining genes in one set (haploid) of the autosomes, and if in their relationship 1F is greater than 1M but less than 2M, then in those classes in which the male is digametic

(FX) (FX)MM is a female because $2F > 2M$
(FX) Y MM is a male because $1F < 2M$

In the classes in which the female is digametic it is necessary to place the male-determining genes on the X and the female determining genes on the autosomes,

(MX) (MX)FF is a male because $2m > 2F$
(MX) Y FF is a female because $1 M < 2F$

and in either case in those circumstances in which the quantitative balance between the male and the female determining genes is such as to lead to a situation in which M = F, intersexuality will result.

But it is to be understood that this is but a way of explaining an imperfectly understood subject concerning which there is a profound lack of physiological knowledge. It would appear to be an established fact that in *Drosophila* the effective factor in the establishment of maleness, femaleness, and intersexuality is the numerical ratio of X-chromosomes to autosomes. Underlying the above explanation is the difficulty that as yet actual differences, as estimated by differences in the chemical nature of the products of their functioning, undoubtedly exist in different types of chromatin organization (genes) and in different gene associations (chromosomes). The chromatin of the X-chromosome is physiologically different from that in the autosome but as yet this difference cannot be defined. At present all that can be stated is that the difference is such that more or less X-chromatin (and also of IV chromatin) in association with more or less A-chromatin leads to one of three types of internal environment in the zygote and its cells, maleness, femaleness, and intersexuality.

In a yellow stock of *Drosophila melanogaster*, L. V. Morgan (1925) found an individual in which the two X-chromosomes were joined end-to-end and from this a stock was raised. It will be seen that so long as this double-X remains unbroken such a female will elaborate two sorts of egg, one carrying the double-X and the other lacking an X. A double-X egg fertilized by an X-bearing sperm will yield a triplo-X super-female. The same egg fertilized by a Y-bearing sperm will yield an XXY female. This double-X chromosome, however, is liable to break at any point along its length. Mul-

ler and Dippel (1926) have shown that by exposure to X-rays artificial breaks of this chromosome can be caused, and that under these circumstances the break is at or near the point of juncture of the two X's. Natural breakage results in a J-portion longer than the normal X and a shorter portion which, owing to the fact that it includes no points of attachment for the spindle, is lost. The XXY female will elaborate XX:Y:J ova. The J-bearing ovum fertilized by a Y-bearing sperm yields a normal male.

Muller and Dippel point out that during the course of the elaboration of these ova there were involved tissues which possessed an XY type of genotype like that which occurs in ordinary diploid male cells, and like the spermatogonia themselves, and they express surprise that cells of identical genetic composition and in an identical environment may thus pursue entirely different modes of development. They point out that cells of male genetic composition metamorphose into ova not because of any special substance or influence exerted upon them derived from other cells of the female body, and not because of any egg-forming substances that might be present within their own protoplasm, derived from an earlier period in which they possessed the female gene complex, but because, they would suggest, the processes of oogenesis really—chemically—begin in much earlier germ cells than the oocytes and that after the early period in which oogenesis is initiated, each step in the process in turn produces the next reaction of the series in chain-like connection until the definitive ova are laid down without the further direct intervention of the genetic determiners that decided the nature (whether male or female) of the original reactions.

TABLE 3

	MALES	FEMALES	INTERSEXES
Sex combs on forelegs	Present	Absent	Absent
Number of dorsal abdominal tergites	Five	Seven	Seven
Ovipositor	Present	Absent	Present
Spermatheca	None	Two	Two
Penis	Present	Absent	Absent
First genital tergite	Present	Absent	Present
Anal plates	Lateral	Dorsal ventral	Lateral
Claspers	Present	Absent	Present
Tip of abdomen	Black	Banded	Black
Gonads	Testes	Ovaries	Very minute
Sex-chromosome constitution	XY	XX	XX (even those parts with male chacterization)

It will be argued in this paper that the form of the gamete is determined by the organization of the gonad, this being determined by the initial general or local genotype, and that the genotype of the gamete has no relation to its form or function.

B. Disharmony in the composition of the genotype

1. A "gene" for intersexuality in Drosophila simulans. Sturtevant (1920) has shown that there is a single recessive chromosome II gene which when in the duplex state turns females into intersexes and renders males sterile. Two hundred

of these intersexes appeared in a stock and unlike the rather variable polyploid intersexes of *Drosophila melanogaster* were all of a definite and constant type. Their characterization is detailed in table 3.

Matings between the stock that gave the intersexes and others that did not, gave no intersexes in F_1, but these appeared in F_2. Pair matings within the intersex-producing stock gave 510 females; 165 intersexes; and 754 males, an excess of males and a 3:1 ratio in respect of sexual normality and sexual abnormality. This character intersexuality is linked with the chromosome II recessive character plum, for three F_1 females out of an intersex × plum mating gave in F_2

Females:	
Wild type	Plum
198	91
Intersex:	
Wild type	Plum
87	0
Males:	
Wild type	Plum
293	65

There was no intersex plum class, showing that these characters are linked, that their genes are resident in one and the same chromosome.

These cases are of the utmost importance in that they show that intersexuality can be caused by a genetic and stable reorganization of the chromatin in a single locus in a chromosome and that this in its effects is sufficient to transform the state of femaleness which would have become established in its absence into one of stable intersexuality. It is of interest to note that the duplex state of the gene is required to produce this result in the female, whereas in the male it leads only to a genetic type of infecundity. It should be understood that by a gene for intersexuality is meant that a certain organization of the chromatin in a particular area of a particular chromosome, different from that organization of the chromatin in this area that is associated with the development of a normal sexual characterization, produces in its action, through its physiological contribution to the general economy of the zygote, a disturbance in the internal environment so that this no longer is characterized by those properties which can be summed up as femaleness but becomes altered in the direction of maleness.

It will be noticed that certain of the component structures of the sexual characterization of the intersex are completely female and that others are completely male. There is no intermediate characterization of parts. That this is so might conceivably be explained in one of two ways. The zygote is a genotypic female 2X:2A in chromosome constitution but on two of the autosomes there is the gene for intersexuality. Every cell of the body will contain the same genotype. The internal environment of every cell is the same yet some tissues differentiate according to the architectural plan of the male, others to that of the female. It may be that certain tissues are more susceptible to the stimulus of the modified environment. But another explanation and one that seems to be more reasonable is that which assumes that there is a time seriation in differentiation, those structures that assume the male characterization becoming differentiated earlier or later than those that assume the female characterization, and that the gene for intersexuality comes into action when one or other set has completed this differentiation. The intersexes would then be intersexes in time. The suggestion that all the component genes in a genotype do not come into action is not extravagant; it is more pleasing than that which demands a varying potency of genes. The conception that the genotype is to be regarded as an unbolting mechanism, the units of which come into action serially

and evoke responses in tissues that exhibit a seriation in the time at which they can respond will be discussed later.

2. Serial Intersexuality in Lymantria. It has long been known (Standfuss, 1896) that when species or even geographical races of Lepidoptera are crossed sexual abnormalities commonly are found among the hybrid offspring. For example, if European specimens of the notorious forest pest, *Lymantria dispar*, the gipsy moth, are bred among themselves the offspring are unremarkable in every way. The same is true in the case of the Japanese variety, *Lymantria japanica*. But if a Japanese male is mated with an European female, normal male offspring and females that show a number of modifications in the direction of maleness, i.e., females that are intersexual, are produced. When such female intersexes were fecund, i.e., were not too abnormal, and were mated with their brothers, it was found that in the succeeding generation typical Mendelian segregation occurred, half the females being sexually normal, half being intersexual. The reciprocal cross, European male and Japanese female, produces normal males and females in the first crossbred generation, but if these are then interbred there appear in F_2 a certain proportion of males that show modification in the direction of the female type of organization, i.e., males that are intersexual.

Further investigation by Goldschmidt (1923) and his associates demonstrated that there were many different races of European, Japanese, and American gipsy moths that were quite distinct in their hereditary constitution in respect of this character intersexuality, in that the degree or grade of intersexuality was definite and typical for a particular mating. As the result of much experimental breeding work Goldschmidt was able to classify his strains as relatively "strong" or "weak." For example, a "strong" male mated to a "weak" female would give 50 per cent normal males and 50 per cent intersexual females. A very "strong" male mated to a "weak" female would give offspring all possessing the male type of sexual organization. A mated to B gave low grade of intersexuality, C × D a high grade, E × F a grade intermediate between these, and so on. If strong race A gave moderate intersexuality with weak race P, while with race Q it gave strong intersexuality, and if strong race B gave moderate intersexuality with Q then it could be predicted that B with P would give only a slight grade of intersexuality. Similar males from one culture mated with females from different cultures gave intersexes that could be arranged in a series according to the degree of their abnormality: males from different cultures mated with females from one and the same culture gave intersexes that differed from these but which could also be arranged in a series. It was possible, by calling on experience, to produce at will every stage from an almost complete male to an almost complete female intersex by making the appropriate mating. In fact, it was as possible to turn the genotypic females into phenotypic males as to ensure the regular production of normal males and females.

It was noticed that the condition of intersexuality did not affect all the structures of the sexual organization equally. Some were normal, while others were intersexual in their characterization, and only purely quantitative characters, such as the length of the antennal pennae, exhibited a condition intermediate between those of the normal male and female. Further investigation demonstrated that the different structures could be arranged in a definite series as regards de-

velopment of intersexuality in characterization and that this series was exactly the opposite to the order of the embryonic differentiation of these structures. Those organs which are the first to be developed and differentiated are the last to be modified; those that appear last are the first to be changed. From these considerations there arose the Time Law of Intersexuality. An intersex is an individual that has developed as a male (or female) up to a certain point in its life history and thereafter has continued its development as a female (or male). The degree of intersexuality is determined by the time during the critical period of sexual differentiation at which this switch-over occurred.

The intersexual females start their development as females and then at a certain point in their development change their mode of differentiation and finish as males and since the hard parts of an insect are external and composed of chitin any of them that have hardened before the switch-over remain unaltered by it. From an examination of the parts which are sexually dimorphic, it is possible to decide in the case of any particular individual exactly when the change-over took place. The intersex is a sex-mosaic in time. The female showing the least degree of intersexuality has only the feelers modified in the manner of the "feathered" male type. Those displaying a further degree of intersexuality will have the male coloring of the wings in addition. A further stage will consist in the addition of a male type of copulatory organs. Next will be a male-type abdomen, and the final stage of all will be that in which the ovaries are replaced by testes, i.e., the genotypic female (according to chromosome content) will have become a phenotypic male, i.e., an XY individual has assumed the characterization normal in one with the XX type of chromosome constitution. The fact that an individual primarily equipped with ovaries can become so transformed as to possess testes is of profound interest since it illustrates in the clearest possible manner the relation of the structure of the gamete to the organization of the individual producing it. Genotypically the sperm will be identical with the ova previously produced but structurally and physiologically they will be profoundly dissimilar. The genotype of the zygote decides the organization of the gonad and this decides the morphological and physiological properties of its manufactured product, the egg or the sperm. It is not the genotype that distinguishes egg from sperm; they differ because they are the products of dissimilar gonadic organizations and the difference takes the form of dissimilar structure and behavior.

From these facts Goldschmidt deduced the following conclusions:

(1) Each sex possesses the potentialities of the other since either can become intersexual. (In other words, the embryonic tissues are ambivalent as regards their future sexual differentiation).

(2) The type of sexual differentiation that the zygote will pursue is determined at the time of, and by the mechanism of, fertilization. (In other words, sex is determined by the nature and interaction of the genotype established in the zygote by the conjugating genes. If the genetic ingredients of intersexuality are in the zygote, then the individual will inevitably become an intersexual form).

(3) The normal determination of sex is bound up with the X-2X mechanism. But as this does not prevent the occurrence of intersexuality and the transformation of one sex into the other, it cannot be the mere presence of these chromosomes or the factors contained within them that counts, but rather their quantitative effect.

(This is in line with the conclusions that have emerged from the consideration of other forms of intersexuality discussed earlier in this paper).

(4) The mode of inheritance of this intersexuality shows that since the female in *Lymantria* is XY, and since her single X-chromosome is received from her father, one of the deciding factors in sex-determination is transmitted in the X-chromosome. (This is in line with previously formed conclusions).

(5) Other factors concerned in sex determination in *Lymantria* are purely maternal in inheritance, being resident in the Y-chromosome. A daughter receives her Y-chromosome from her mother. But since a male has no Y-chromosome, the factors in the Y-chromosome must have exerted their action on the unripe egg when this contained both X- and Y-chromosomes. (It will be remembered that the mature egg of a female that is digametic carries either an X or the Y. This is due to the fact that of this XY pair one member passes into the polar body whilst the other stays in the egg. The eggs will therefore be of two sorts, X-chromosome bearing and Y-chromosome bearing, the former being fertilized by the X-chromosome bearing sperm and giving rise to an XX individual, a male, the latter being fertilized, to an XY zygote, a female). If all eggs are to be alike in respect of the Y-borne genes these must have acted and their products must have specifically affected the cytoplasm before the X and Y became disjoined. It is seen then that there is good reason for postulating that different genes come into play at different times. It is to be noted that the Y-chromosome of *Lymantria* is not as the Y of *Drosophila*, it is not physiologically inert but resembles the Y of fishes in that it carries active genes (Aida, 1921, Winge, 1922).

(6) The fact that the genetically similar females give different results when mated with genetically dissimilar males shows that the sex-determining genes in the X-chromosome differ quantitatively in the different races. The fact that genetically similar males give different results when mated with genetically dissimilar females shows also that the sex-determining factors resident in the Y-chromosome can be different quantitatively.

It will be seen that if both X-borne and Y-borne sex-determining genes can so vary quantitatively among themselves an infinite variety of different genetic combinations can be made, deliberately or by chance.

In order to explain his results and his hypothesis Goldschmidt developed a somewhat intricate presentation. To the male-determining tendency of a particular race he assigns a positive value that is proportional to the strength of the male-determining genes. To the female-determining tendency he assigns another value also proportionate to the strength of the female-determining genes. He then assumes that when in an individual the male value is greater than the female value by a certain number of units the individual is a male and that conversely when the female value is greater than the male by a certain number of units the individual is a female ($F - M = > 20$, a female; $MM - F = > 20$, a male). In a weak race, for example, F, the female-determining gene complex, has a value of 80 units assigned to it and M has 60. Since the male-determining gene-complex M is borne on the X-chromosome and the female-determining gene complex F is in every egg in the female, XY in constitution, F 80 exceeds M 60 by the epistatic minimum of 20 units, and the individual therefore becomes a female; in the XX

males, on the other hand, M = 60 + 60 as against F = 80, so that there is an excess of 40 units in the male direction. In a strong race F is 100, M is 80, but the arithmetical relation between the values of F and M still governs the sexuality of the individual. (It should be stated that it does not seem impossible to restate the whole argument in terms of a numerical ratio as Bridges has done in the case of *Drosophila*. This algebraic interpretation is not really satisfactory).

since they come from different sources (see table 4).

By the use of such symbols it is easy to illustrate the production of an F_1 generation consisting of 50 per cent males and 50 per cent females whose bodily characteristics are male (see table 5).

Goldschmidt infers with reason that the sexual characterization of any particular organ of the sex equipment depends on whether one or the other type of sex-differentiating substance is effectively in

TABLE 4

RECIPROCAL CROSS

A weak male	$M_2M_2F_3$	M_2mF_4	A strong female	
Gametes	M_2	$M_2F_4 : mF_4$		
F_1	$M_2M_2F_4$ M>F therefore ♂	M_2mF_4 M<F therefore ♀		
Gametes	M_2 M_2	M_2F_4 mF_4		
F_2	$M_2M_2F_4$ / Intersexual male	M_2mF_4 / Female	$M_2M_2F_4$ / Male	M_2mF_4 / Female
	M = F	M<F	M>F	M<F

> = greater than; < = less than.

TABLE 5

P_1, strong male	$M_5M_5F_8$	M_5mF_8	Weak female
Gametes	M_5	M_5F_8 mF_8	
F_1	$M_5M_5F_8$ / Male M > F	M_5mF_8 / Female (MmF) but M > F, so all with male organization	

The conception of Goldschmidt can be illustrated by assigning arbitrary numerical symbols to the sex-determining factors. M = male-determining gene resident on the X-chromosome. M_1, M_2, M_3, M_4, M_5, etc. are male-determining genes of relatively different efficiencies; M_1 is a weak M, M_5 a relatively very strong M, and so on. Since a male has two X-chromosomes he carries two M's and these may be of different grades of efficiency,

excess at the time when the organ arises in development. He interprets the mosaic character of the intersex by the assumption that the amount of sex-differentiating substances produced in virtue of the presence of the corresponding sex-determining genes is not constant throughout life: that at one time the male-differentiating substance is in excess, at another the female. In the male of the moth M > F and the male-differentiating substance

is effectively in excess until the period of differentiation is compl ted. In the case of the female M < F and the female-differentiating substance is effectively in excess during development. But if it should so happen that the sex-differentiating substances are produced at different rates, and if some genes possess the property of producing more sex-differentiating substance in a given time than others, then there exists the possibility that sex mosaics in time will be produced.

A male of a race in which the sex-determining genes work at a faster rate is crossed with a female of a race in which these genes work at a slower rate. The female-determining factor F is always inherited through the mother and in all the offspring there will be this factor F and the female-differentiating substance will be produced in all at the same rate. The male offspring, on the other hand, will receive one M from their mother, and the other, the quickly producing M, from their father, so that in a given time the male-differentiating substance will be effectively in excess during development. The female offspring will have the M from the father, and as a consequence the amount of male-differentiating substance will increase relatively to the amount of the female-differentiating substance, overtake it, and finally supplant it, and from this point onwards any sex-characters which still have to develop will be of the male type. The individual will be a female intersex. It is not the absolute but the relative rates of production of male- and female-differentiating substances that control the modelling of the sex-equipment, as shown in Figure 9.

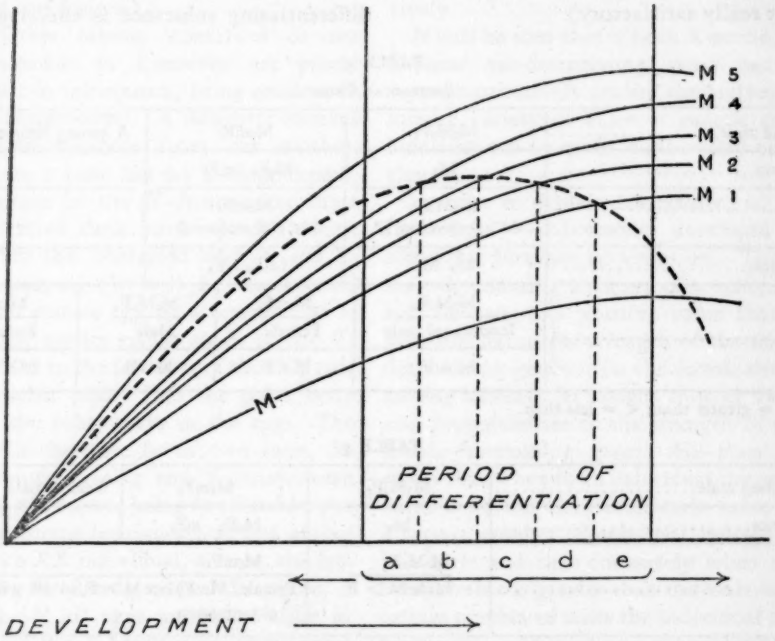


FIG. 9. THE TIME LAW OF INTERSEXUALITY (AFTER GOLDSCHMIDT)

There are two sorts of sex-determining

genes, male-determining, borne on the X, and female-determining, borne on the Y. The male genetically is MMF and the female MmF, since the action of the Y-borne genes is prezygotic. The sex-determining substances elaborated by these genes are known as male-differentiating and female-differentiating substances. These are elaborated at different rates by different male-determining and female-determining genes respectively; the introduction of more quickly and of more slowly elaborating genes into a genotype can result in a disturbance of the previous quantitative relation of the two sorts and so yield the intersexual condition.

In general the point at which the curves for production of the male- and of the female-differentiating substances intersect lies beyond the stage at which differentiation occurs. But if the growth rate could be changed so that the point of intersection occurred during or before the period of differentiation, then it should be possible to produce a partial or complete reversal of sex and to produce individuals genetically of one sex (XX or XY, that is), but somatically, phenotypically of the other. Goldschmidt by rearing *Lymantria* at very low temperatures produced intersexes, thus verifying this inference. Sex-reversal in these cases is due to genetic causes—the fertilized egg contains inevitably within itself the seed of its eventual transformation in the form of a quantitative disharmony of the sex-determining factors.

In the case of *Lymantria* the situation can be summarized as follows. Genetic intersexuality is the condition in which as a result of genetic causes the differentiation of the sex-organization of a genotypic male or of a genotypic female, having been pursued up to a point in a manner appropriate to that sex, is switched over, so that after this point it follows the plan appropriate to the opposite sex. An intersex is an XX (or XY) individual which, as a result of an abnormal sexual differentiation comes to possess more or less completely the sex equipment appropriate to the alternative XY (or XX) individual. Not every part of the body is involved in this condition; only the structures of the sex equipment are concerned and of these only those are affected the differentiation of which is not complete at the time of the switch-over; the earlier in development the switch-over occurs, the more structures will be affected and the greater will be the degree of the intersexual condition, and *vice versa*.

Intersexuality results when the male and female sex-determining genes are quantitatively incorrectly in harmony, one set with the other. It does not occur when, as in the case of the genotypic female which attains a typical female organization, the female-determining reactions are predominant throughout the period of differentiation. Intersexuality occurs when during the course of this phase of differentiation the male-determining reactions overtake and supplant the female-differentiating reactions and so control the remainder of the process, or when the female-differentiating reactions replace the previously predominating male reactions.

Under ordinary circumstances the female sex-differentiating substances in the male or *vice versa* are produced so slowly that an effective quantity is not present until the critical phase of differentiation has closed. If, however, their production were speeded up through the presence and action of a more rapidly producing female gene-complex, the time point at which these female-differentiating substances attained effective supremacy would fall within the critical period of differentiation and would then be the switch-over point. Each fertilized egg normally pos-

sesses male and female-determining genes which elaborate enzyme-like and specific sex-differentiating substances. In species in which the female has the constitution symbolized as XY, the female sex-differentiating substances are purely maternal in their mode of transmission so that every egg produced by one and the same female is identical in respect of this. The male-determining gene-complex is X-borne, and, therefore, is present in half the eggs and in all the sperm. The rate of production of the two sex-differentiating substances or the time at which they come into action is a fixed hereditable character of a race.

The case of *Lymantria* is of particular interest because it provides strong evidence that there are genes on the Y-chromosome and that different genes come into action at different times during development. It is seen that in *Lymantria* the Y-borne genes are not concerned with the development of morphological characters directly but with the establishment of a certain metabolic level. In the case of *Drosophila* it is known that the Y-chromosome is not concerned in the development of morphological characters but that its presence is necessary if the male is to be fecund. It is possible that the Y-chromosome of *Drosophila* does carry genes and that these, like the Y-borne genes of *Lymantria*, are concerned with the establishment of physiological characters exerting their action before organogeny commences.

It is important to note that though the phenomena of intersexuality in *Lymantria* are commonly interpreted as the results of genetic difference in the rate of production of sex-differentiating substances, it is equally satisfactory to explain them as the sequelae of genetic differences in the time at which different gene complexes concerned in sex-determination come into action during development. M_1 and M_5 would then be equally potent, but M_5 would come into action earlier. In this connection the work of Hartmann (1925) on the plant *Ectocarpus siliculosus* is well worthy of reference.

The researches of Pflüger (1882), Hertwig (1912) Schmidt-Marcell (1908), Kushakevich (1910) and Witschi (1914-1915) have revealed the fact that in the frog there are two forms of development of the reproductive organs. In one the differentiation of the gonad is either that which leads directly to the organization of an ovary or that which directly yields a testis. In the other there is in the beginning an organization that is female in its characterization but sooner or later 50 per cent of these cases become transformed into testes. It has been established that this tendency to early and direct differentiation on the one hand, and to late and indirect differentiation on the other are truly heritable characters and that the hereditary factors for these characters can be transmitted by either father or mother; breeding experiments yielded results closely resembling those obtained in the mating of individuals of different "efficiencies" of *Lymantria*, and there is good reason for interpreting these temporary intersexuals in terms of Goldschmidt's *Lymantria* hypothesis. Swingle (1925) very ably upholds the view that the early gonad of the male of indirect and late differentiation is not ovarian and that such a male is not an intersexual. He argues that this progonad is sexually neutral in consequence of a balance between male and female determining tendencies in the zygote and the fate of the progonad is decided when the definitive sex-cords appear, for then the progonad becomes transformed into a testis. The definitive testis cannot develop in the absence of sex-cords and the appearance

of these decides the course of development. The time of the appearance of these peculiar male structures, the sex-cords, is probably determined by genetic factors and so different races and their hybrids differ in the time at which progonad becomes testis. According to Swingle "Pflüger's hermaphrodites" are but males in which the appearance of sex-cords in the progonad is greatly retarded and many recorded cases of sex reversal in the frog and toad are but instances of such retardation.

It is of considerable interest to note that Witschi secured an adult hermaphrodite the eggs and sperms of which were used. The eggs of this hermaphrodite fertilized with sperms from an individual of a race in which early and direct differentiation was the rule yielded males and females: sperms of the hermaphrodite fertilizing eggs of a female of a race in which early and direct differentiation was the rule gave only females. These facts point to the conclusion that this hermaphrodite frog was XX in sex-chromosome constitution and that all its gametes, eggs and sperms alike, contained a single X. The X sperms fertilizing the X eggs of the monogametic female yielded only XX individuals: the X eggs being fertilized by both X and Y sperms gave both males and females. It is to be noted that here again is an instance of egg and sperm being genotypically equivalent, of ovary and testis being possessed of the same genotypic constitution. Manifestly though an individual that has the sex-chromosome constitution XY develops testes, these develop not because they are XY but because they developed in a particular kind of internal environment that the interaction of the genes in an initial XY genotype established.

Hertwig and Witschi were able to show that temperature has a definite influence on the type of gonadic differentiation in frogs. They found that certain forms cultivated at 21°C showed early and direct gonadic differentiation, whereas when cultivated at 27°C some of the females changed after the metamorphosis into males. In another race cultivated at 27°C all these females became transformed into males. Evidences of this transition in sexual differentiation can be obtained from other sources. At the anterior end of the testis of the toad is Bidder's organ, a rudimentary ovary. It is found in both sexes while the individuals are immature but in the case of the female it degenerates. Harms (1914) was able to show that Bidder's organ was a rudimentary ovary and that it possessed an endocrine function. All the males of *Perla marginata* possess a well developed but non-functional ovary anterior to the testis (Schönemund, 1912). In *Phyllodromia germanica* Heymons (1890) has demonstrated that the anterior part of the gonad of the male is differentiated into ovarian tissue; in *Orchestia* Nebeski (1880) has shown that a part of the testis always contains eggs; while in the crab, *Gebia major*, Ischikawa (1891) has shown that the anterior part of the gonad of the male is testicular whereas the posterior portion is ovarian though incapable of functioning. In *Myxine* Schreiner (1904) has shown that while no real hermaphroditism occurs, the gonad is mixed, though only the testicular or the ovarian tissue is functional. The work of Grassi (1919) on the eel suggests that similar conditions obtain in this form.

These and many other cases can be interpreted by an appeal to the hypothesis of Goldschmidt.

If it is agreed that the essential difference between the male and the female lies in the timing mechanism which decides whether, while a given organ is developing, the male or the female

determining reactions are predominant, if it is agreed that at some point in the development preceding or following the stage of differentiation the female determining reactions are predominant in a genotypic male and *vice versa*, then the efficiency of environic agencies to cooperate with the genetical factors offers no difficulty. The provisional hypothesis outlined by Goldschmidt to account for his *Lymantria* intersexes then brings into one coherent scheme undoubted sex-transformation as seen in *Crepidula*, *Sacculina*, and *Bonellia*, the occurrence of oviform cells in the protestis of *Anura* (or among Myriapods as steps in normal spermatogenesis), and the cases of sex-reversal met with in birds.

Bidder's organ, for example, can readily be interpreted on Goldschmidt's hypothesis. A represents the progonad; B the definite testis. It will be remembered that the development of the progonad is actually later in the forms with a protracted larval phase. During the earlier part of the development of the individual the female-determining reactions are predominant, the female-determining substances are effectively in excess, and any organ that is developed during this period and is responsive to the action of their stimulus will pursue its development and differentiation under their direction; later, in the case of the determined male, the male-determining substances become effectively in excess, and all differentiation of the structures of the sex-organization will

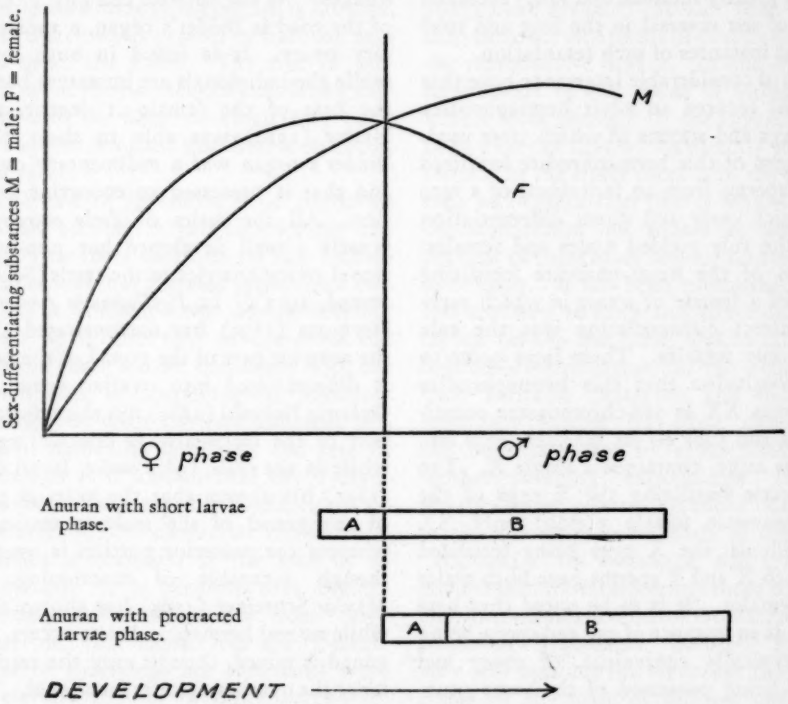


FIG. 10

Fig. 10 shows how the significance of

thenceforward be according to the male plan. Thus it will happen that in the case of the Anuran with a short larval phase, the progonad will present the characteristic features of Bidder's organ, whereas in the case of the Anuran with a protracted larval life, in which the progonad is developed later, there will be no Bidder's organ and no ovum-like bodies in the testis.

Other somewhat similar instances of intersexuality that must await interpretation until it has been shown whether they fall into the *Drosophila* or *Lymantria* categories have been recorded by Harrison and Doncaster (1914), Kuttner (1909), Banta (1916), de la Vaulx (1921), Sexton and Huxley (1921), and by Keilin and Nuttall (1919).

3. Intersexuality in the mammal.

(a) Intersexuality due to abnormality in the time of the differentiation of the gonads. Abnormality of the reproductive system taking the form of an intimate mixture of male and female structures belonging to the accessory sexual apparatus is not uncommon among the domesticated mammals, and many cases have also been recorded in the human subject. The typical history in these cases is that an individual, regarded as a female during the earlier part of its life, later assumes many of the characters of the male. This peculiar type of abnormality is particularly common in the goat and pig. In the goat cases are known in which an individual which actually won prizes when shown as an immature female, from the time of sexual maturity became more and more like the male: its beard grew, its head became male-like, and about it there hung the pungent smell so characteristic of the male. In its behavior it resembled the "rig," a male with maldescended testes, but its external genitalia retained the form of a vulva-like aperture with an overlarge clitoris. When the internal genitalia from such a case are examined there are found paired gonads lying in the situation of ovaries or somewhere along the track of the migrating testes, which on section show the structure typical of the maldescended testis; and an accessory sexual apparatus composed of more or less well defined epididymes, vasa deferentia, seminal vesicles, prostate, Cowper's glands, uterus, and vagina, the latter in some cases having failed to establish communication with the vulva.

The literature contains many references to this type of abnormality in the human, goat, and pig, but these were treated as isolated examples and no successful effort was made to give to them a common interpretation until Crew (1923) examined a considerable number of cases in the goat, pig, horse, cattle, sheep, and camel. In a few of the cases examined, the external genitalia had the form of an unremarkable vulva and clitoris; in others the rectile organ though female in form was unusually large and prominent; in others it was distinctly peniform yet imperfectly canaliculized. In a few instances there was a solid conical elevation on the abdominal wall where in the normal male the penis ends.

In all cases the differentiation of the Müllerian and Wolffian derivatives was imperfect, and the accessory sexual apparatus consisted of an intimate mixture of more or less well developed male and female structures. The most variable in its degree of development was the uterus.

It was found on examination that the cases of this condition in the pig fell cleanly into one of two classes, (1) those in which no morphological evidence of the previous or present existence of ovarian tissue could be found in the gonads which were entirely composed of testicu-

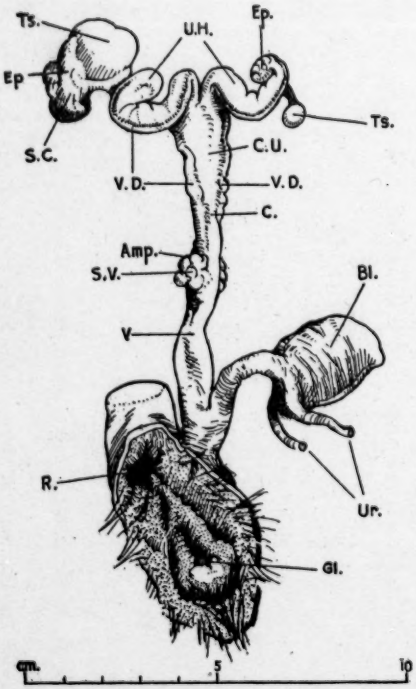


FIG. IIA

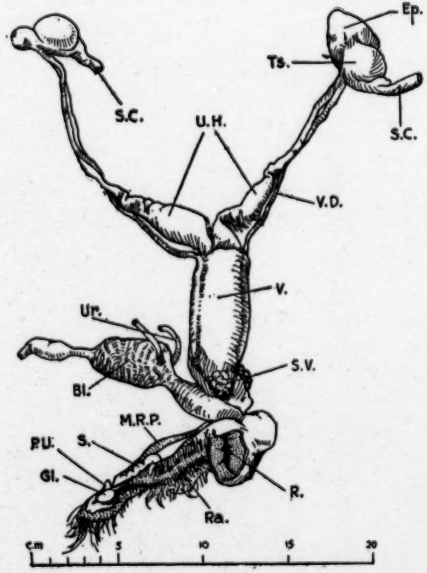


FIG. IIB

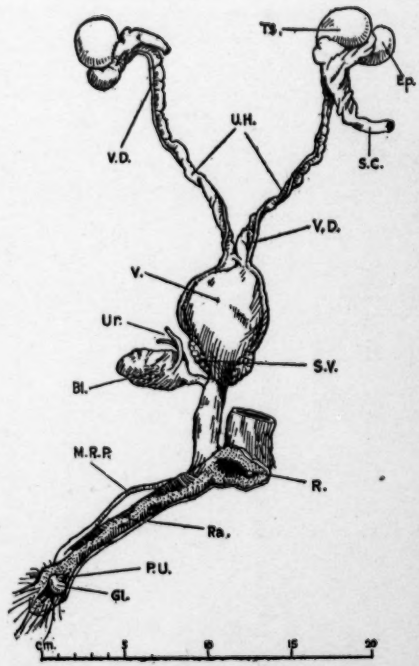


FIG. IIC

FIG. IIA, B, C. TYPES OF INTERSEXUALITY ENCOUNTERED IN THE GOAT

Amp., ampulla of vas deferens; *Bl.*, urinary bladder; *C.U.*, body of uterus; *Cl.*, clitoris; *Ep.*, epididymis; *Gl.*, glans penis; *M.R.P.*, retractor penis; *P.U.*, processus urethrae; *R.*, rectum; *Ra.*, median raphe of perineum; *S.*, flexures of corpus cavernosum penis; *S.C.*, spermatic cord; *S.V.*, seminal vesicle; *T.*, testis; *U.H.*, uterine horns; *Ur.*, ureters; *V.*, vagina; *V.D.*, vas deferens; *Vu.*, vulval cleft.

lar tissues with a histological structure varying with the position of the testis along the line between the primitive position and the scrotum, but always exhibiting some degree of degenerative change; and (2) those in which both ovarian and testicular tissues were present, the gonads being one an ovary, the other a testis; one an ovary, the other an ovotestis; or both being ovotestes. In one case there were paired ovaries within the abdominal cavity and paired testes beneath the skin of the perineum.

It was noted that in the cases of class 2 in which one gonad was an ovary, this gonad was always the left one, and that in an ovotestis the ovarian tissue was invariably cephalad to and sharply separated by a well defined belt of connective tissue from the caudad testicular portion. The ovarian tissue was invariably of apparently normal structure histologically, whereas in the testicular tissue the spermatogenic was always degenerate to some degree and the interstitial plentiful.

Those individuals in which the external genitalia were distinctly abnormal had been identified as "hermaphrodites" or "wilgils" by the breeders, and had been slaughtered while still immature. The few in which the external genitalia had the form of an unremarkable vulva and clitoris had been regarded as females until about the time of sexual maturity, when it was noted that instead of assuming the sexual characterization of the adult female they had begun to exhibit the secondary gonadic characters of the male type, and that the clitoris had begun to increase in size. The sexual behavior of such of these individuals as proved later to belong to class 1 was as that of the "rig," a male with maldescended testes. The behavior of such as belonged to class 2 was imperfectly male. They were slaughtered because of their curious behavior and because they failed to breed.

The fact that in one class of these cases of reproductive abnormality there is no ovarian tissue and no suggestion that there ever had been any, whereas in the other class there is ovarian tissue of apparently normal structure, points to the conclusion that the two classes are different in their nature. If ovarian tissue had ever been present in the case of class 1, it should have persisted, since in those cases in which ovarian tissue is present it is invariably of normal structure. It is proposed to regard the two classes as being distinct and to treat them separately.

During ontogeny there is a period in which the differentiation of the sexual organization is timed to take place. At the beginning of this period which follows a preliminary phase of growth and organ formation, the reproductive system consists of (1) paired gonads of indifferent histological structure; (2) a rudimentary accessory sexual apparatus composed of Müllerian and Wolffian ducts; (3) external genitalia represented by the growing urogenital sinus and genital tubercle. From this initial type of reproductive architecture, possessed in common by all individuals, genotypic male and female alike, one or other type of differentiated sexual organization, male or female, is attained. The indifferent gonads become testes or else they become ovaries; if they become testes then the Wolffian ducts continue their development to become the functional deferent ducts of the testes, while the further development of the Müllerian ducts ceases and the external genitalia become scrotum and penis. If the indifferent gonads become ovaries the Müllerian ducts continue their development to become the functional uterus with cornua and Fallopian tubes and vagina, while the develop-

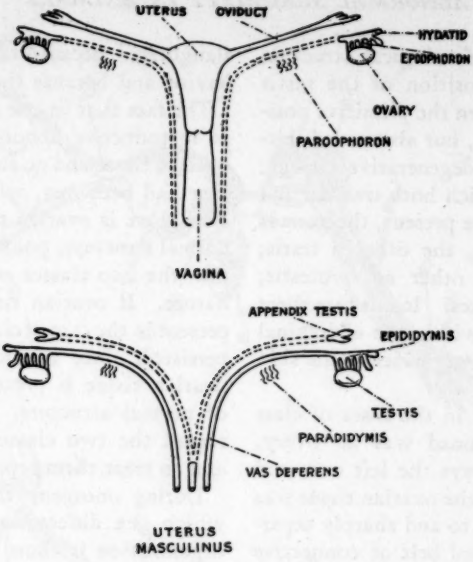


FIG. 12A

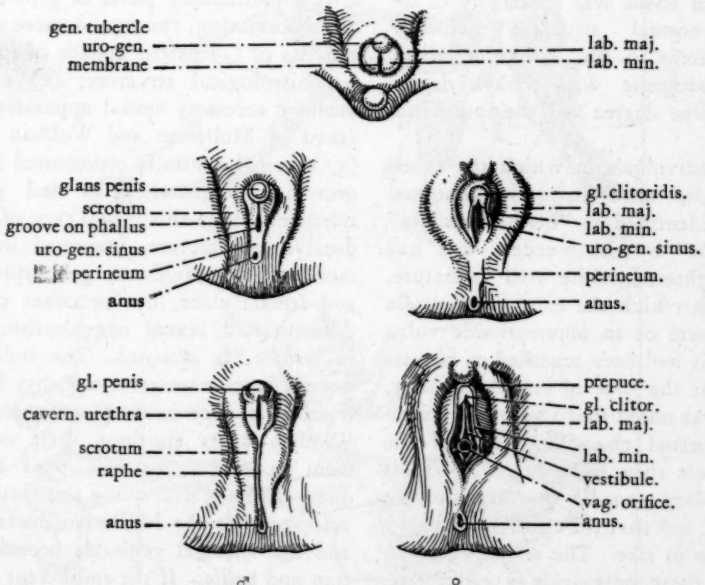


FIG. 12B

FIG. 12A, B. DIAGRAMS ILLUSTRATING THE ALTERNATIVE DEVELOPMENT OF THE INTERNAL AND EXTERNAL GENITALIA FROM A COMMON EMBRYONIC TYPE

A, the internal genitalia (after Broman); *B*, the external genitalia (after Hertwig)

ment of the Wolffian ducts ceases and the external genitalia assume the form of vulva and clitoris. Sexual differentiation is alternative and the end-product is an organization appropriate to the functional female or else to the functional male.

Between the differentiation of the various structures of the sex-equipment there is a time relation. The first structure to begin its differentiation is the gonad, the next, it is assumed, the external genitalia, and finally the structures of the accessory sexual apparatus. The results of gonadectomy and gonad implantation have shown perfectly clearly that for the appropriate differentiation of the rest of the sex-equipment the differentiated gonad is necessary. In the presence of functional testicular tissue the sexual organization appropriate to the functional male is assumed; in the presence of functional ovarian tissue that appropriate to the functional female. Such differentiation is pursued under the control of specific male and female sex-hormones elaborated by the testis and ovary respectively. Since the different structures of the sex-equipment respond to the physiological stimulus of the sex-hormones at different times during ontogeny it can be assumed that the threshold of response to this stimulus differs in different cases, and that before this threshold of response is reached a certain degree of undifferentiated growth is required. If the effect of the functioning of the differentiated testis is to inhibit the further development of the Müllerian ducts and their derivatives and to encourage the fuller development of the derivatives of the Wolffian ducts and to model the growing urogenital sinus and genital tubercle into scrotum and penis, then it is necessary only to explain the differentiation of the embryonic gonad into testicular tissues in order to explain the complete assumption of a male type sexual organization by the individual.

This can be done if it is assumed that the gonad in its indifferent stage is ambivalent as regards its future mode of differentiation (though not completely so since its tissues are chromosomally either male or female, XO or XX), and that this differentiation is pursued under the direction of male-differentiating and female-differentiating substances elaborated by the male-determining and female-determining factors respectively. In the genotypic male (XO in sex-chromosome constitution) it is the rule for the male-differentiating substances to be effectively in excess over the female-differentiating substances during that period of development when the differentiation of the gonad is timed to take place, whereas in the genotypic female the female-differentiating substances are effectively in excess during this period.

These suggestions can be illustrated graphically as under classifications shown in figure 13.

The interpretations of the conditions found in class 1 can now be attempted. In these cases there were paired maldescended testes, more or less well developed derivatives of both Müllerian and Wolffian ducts, external genitalia ranging from those of the apparently normal female to those of the grossly imperfect male. The cases could be readily arranged in a series according to the degree of imperfection of the external genitalia and of the degree of development of the Müllerian duct derivatives.

The fact that they could be so arranged suggests that they are one and all but grades of the same condition and that between them there exists a time relation. It must be stated clearly that there was no evidence which suggested that the abnormal individuals were free-mar-

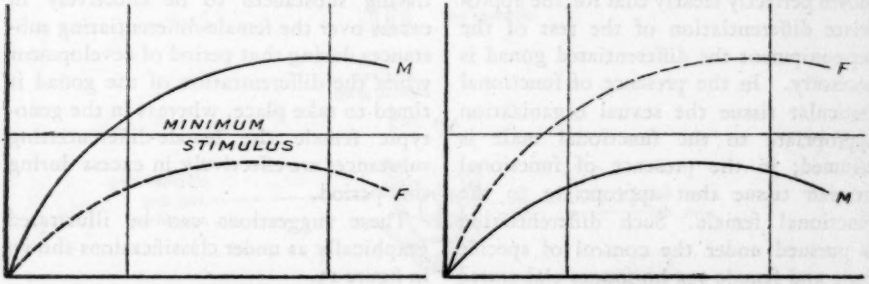
tins (see Part II), cases of sex-reversal in a genetically determined female (see Part II), or cases of true "glandular hermaphroditism" in which the ovarian tissue had been removed at an earlier stage of development. They will be interpreted as instances of abnormal sexual differentiation in the genotypic male and the following assumptions will be made:

(1) The stimulus to differentiation of the remainder of the sex-equipment is, in the mammal, localized in the gonads.

(2) The abnormalities pertain only to the earlier stages of sexual development.

It is recognized that in this differentiation other agencies than the sex-hormone are involved, the other endocrines, for example, and that for effective differentiation there must be appropriate nutrition, but for the present these are disregarded.

For purely descriptive purposes it is assumed that in the process of the differentiation of the sex-organization in a genotypic male, excluding that of the gonads, there are three overlapping phases (1) the modelling of the external genitalia; (2) the atrophy of the Müllerian ducts; and (3) the further development of the



Period of differentiation of gonads.
— Development. →
In the normal male, the male-differentiating reactions are effectively in excess during the whole period of gonadic differentiation, and so the gonads assume the structure of testes.

Period of differentiation of gonads.
— Development. →
In the normal female the female-differentiating reactions are effectively in excess during the whole period of gonadic differentiation, and so the gonads assume the structure of ovaries.

FIG. 13. DIFFERENTIATION OF GONADS

(3) The influence of the gonad in the mammal at this stage is such as inhibits the further development of these structures of the accessory sexual apparatus appropriate to the alternative functional sex, and that these structures, in the absence of such inhibition, would continue their development unchecked.

(4) There exists a different threshold of response to the sex-differentiating stimulus on the part of different structures of the sex-equipment and at different times during the development of one and the same structure.

Wolffian duct derivatives. For the sake of simplicity it is assumed that for all these structures there is one and the same minimum stimulus which, provided by the male sex-hormone elaborated by the testis, will evoke the specific response toward appropriate development. It is also assumed that when once the undirected development of any structure has proceeded for some time then that structure is no longer capable of responding to the stimulus if and when this is exhibited.

In *A*, the minimum stimulus necessary for proper differentiation is exhibited

before the time for differentiation has been reached, and as a consequence the differentiation is such that a completely male organization is established.

In *B*, in consequence of a retardation in the elaboration of the sex-hormone or of the production thereof at a slower rate, the differentiation of the external genitalia is partially undirected, and the result is grossly imperfect external genitalia in an otherwise normal male. The erectile organ will be most affected, for the scrotum of the normal male is sessile, and if in an abnormal male the testes descend through the inguinal canals they will become accommodated in a scrotum very much, if not quite, like that of the normal.

In *C*, in consequence of a greater retardation or still slower production, the end-results will be external genitalia even more imperfect and Müllerian duct derivatives further developed.

In *D*, the external genitalia will be as in *C*, the Müllerian derivatives will be better developed, whereas the development of the Wolffian derivatives will not be so complete.

In *E*, the required stimulus is never exhibited during the period of the differentiation of the accessory sexual apparatus and external genitalia and the end-result will be the full grown embryonic form.

In the absence of the proper endocrine control during the period of differentiation of the accessory sexual apparatus and external genitalia, these structures pursue a parallel development under the common stimulus of nutrition. Epididymes, vasa deferentia, and seminal vesicles develop from the Wolffian duct, uterus and vagina from the Müllerian, and if such undirected growth continues, then after a time these structures will have lost their embryonic plasticity, and will fail to respond to the stimulus of the sex-hormone if and when this is exhibited later. The degree of development of the derivatives of the Müllerian ducts in a male and of the Wolffian ducts in a female and especially the degree of imperfection of the external

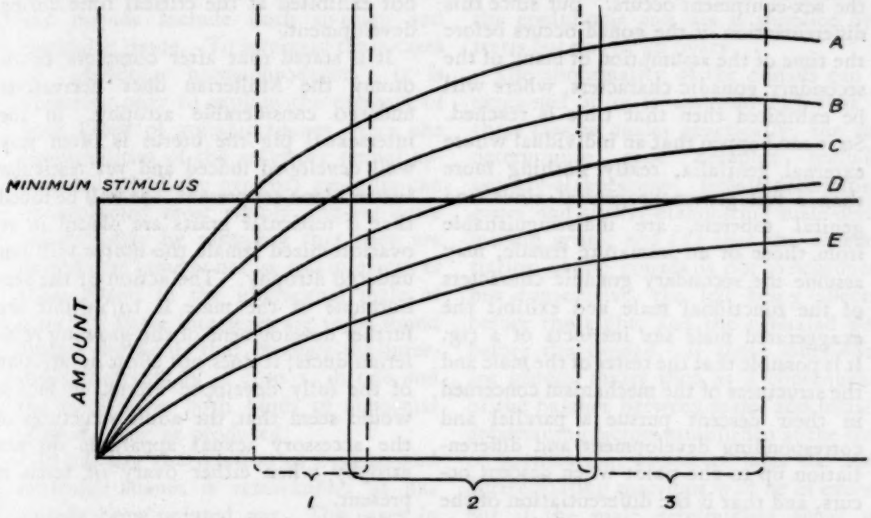


Fig. 14. Speculative Interpretation of the Different Grades of Intersexuality

genitalia in a male, will provide significant indication as to the time during development at which the sex-hormone was exhibited.

These grades of abnormality of the reproductive system in the pig are thus to be explained as the result of the more or less complete absence, or of the qualitative or quantitative insufficiency, of the tissue in which the sex-hormone has its origin during that period of development when the differentiation of the rest of the sex-equipment occurs. But since this differentiation of the gonad occurs before the time of the assumption of many of the secondary gonadic characters, where will be exhibited then that time is reached. So it can happen that an individual whose external genitalia, really nothing more than a full grown urogenital sinus and genital tubercle, are indistinguishable from those of an immature female, may assume the secondary gonadic characters of the functional male and exhibit the exaggerated male sex instincts of a rig. It is possible that the testes of the male and the structures of the mechanism concerned in their descent pursue a parallel and corresponding development and differentiation up to the point when descent occurs, and that if the differentiation of the testis is retarded in any way, the proper association of testis and gubernacular apparatus is prevented or embarrassed so that the maldescent occurs.

The frequency of this type of abnormality in the pig, and the facts that it is more common in certain districts than in others, and that certain individuals in successive matings yield one or more of these intersexual offspring, point to the conclusion that this retardation or insufficiency of the sex-hormone is a character in the genetic sense.

In order to explain this retardation in the exhibition of the sex-hormone the following assumption is made. Different male-determining and female-determining gene complexes elaborate their sex-differentiating substances at different rates or come into action at different times. The intersexual individual of this class is the result of the mating of individuals which transmit to their offspring that sex-determining gene complex in which the factors are "slowly-elaborating" in nature, so that the minimum stimulus for differentiation of the gonad in the male is not exhibited at the critical time during development.

It is stated that after complete ovariotomy the Müllerian duct derivatives undergo considerable atrophy. In the intersexual pig the uterus is often very well developed indeed and yet testicular tissues alone are present. It will be found that if testicular grafts are placed in an ovariotomized female the uterus will not undergo atrophy. The action of the sex-hormone of the male is to inhibit the further development of the growing Müllerian ducts; it does not effect an atrophy of the fully developed uterus, in fact it would seem that the adult structures of the accessory sexual apparatus do not atrophy when either ovary or testis is present.

(*b*) *Intersexuality due to abnormality in the mode of differentiation of the gonad.* The cases in class 2 are instances of as perfect intersexuality as is possible in the mammal. The essential feature of this condition is that both ovarian and testicular tissues shall be present synchronously or consecutively in one and the same individual. The mammal can and occasionally does possess both kinds of gonadic tissues, but it cannot function both as male and female since the external reproductive organs cannot be both male and female in their architecture. Moreover, oogenetic tissue cannot flourish in a scro-

tum nor spermatogenic within the abdominal cavity. Crew (1921) and Moore (1923) have shown that the optimum temperatures for efficient ovarian and spermatic functioning are widely different, and that the temperature within the abdominal cavity is considerably higher than that within the scrotum. Functional hermaphroditism is impossible, therefore, in the mammal.

The cases examined by Crew and those recorded in the literature are similar to those of class 1 in every respect save that the gonads include both ovarian and testicular tissue. To interpret these cases of "glandular hermaphroditism" it is necessary only to explain the presence of both kinds of gonadic tissues, since the abnormalities of the accessory sexual apparatus and of the external genitalia can be explained most simply and yet quite satisfactorily by assuming that they are exactly the same in nature and in origin as those found in the intersexual male of class 1. These intersexes are to be found among the herds that produce the intersexual individuals of class 1; in one and the same litter both kinds of abnormal offspring may be produced.

In the pig the relation of ovarian and testicular tissues is remarkable, as has already been pointed out. The cases in which two ovaries are found within an abdominal cavity and two testes within an imperfect scrotum are to be interpreted as the result of the separation by the gubernacular apparatus of ovotestes. If an ovotestis is thus divided along the line of the connective tissue whch invariably separates ovarian from testicular two distinct gonads will be found on one and the same side of the body. If the testicular portion migrates to a situation beneath the skin of the perineum it might be expected that functional spermatozoa would be elaborated. But even were this the case, the imperfection of the external genitalia would not permit the individual to function as a male.

One point of considerable interest emerges from the study of these cases. If testicular tissue is present in one gonad, testis or ovotestis, an epididymis and vas will be found associated with it, but if the other gonad is an ovary no epididymis and no vas will be found on this side. There is more than hormone stimulation involved: it would seem that some mechanical stimulus to the maintenance of the epididymis and vas is supplied by a testis but not by an ovary.

The abnormality of the gonads can be explained if it is assumed (1) that in these classes, males genetically, the sex-determining gene complex included quickly-elaborating female-determining genes and slowly-elaborating male-determining genes; and (2) that the differentiation of the gonads is not synchronous but consecutive, the left being affected before the right, and the cephalad pole before the caudad. If these individuals are genetic males then as a consequence of the balance between male- and female-determining factors established at the time of fertilization, sooner or later the male differentiating reactions will be in excess, but if the male determining genes are slowly-elaborating and the female-determining genes are quickly-elaborating then the situation will be such that the female-differentiating reactions will first exert the necessary minimum stimulus for gonadic differentiation and ovarian tissue will be laid down, and that shortly the male-differentiating reactions will overtake and replace the female, and the remainder of the differentiation will be pursued under their control, testicular tissues being laid down. The relative amounts of ovarian and testicular tissues will provide an estimate of the time during the period of go-

nadic differentiation when one kind of sex-differentiating reaction replaced the other.

As a result of the simultaneous presence of ovarian and testicular tissues both male and female sex-hormones will be elaborated. It is assumed that this determination of the gonads has been retarded and that before it occurs the accessory sexual apparatus and external genitalia have assumed more or less the full-grown embryonic form. But this differentiation occurs before the time of the assumption of the secondary gonadic characters, and the structures concerned with these will be exposed to the action of both kinds of sex-hormone. The results are as those obtained in the experimentally produced hermaphrodite, a characterization suggesting that certain structures respond preferentially to one sex-hormone, others to the other. The phallus invariably enlarges, while the sexual behavior is exaggeratedly male.

If, on the other hand, the differentiation of the gonads, though abnormal in its mode, is normal in time, occurring before the differentiation of the rest of the sex-equipment is timed to take place, the situation can arise in which, owing to the presence of both ovarian and testicular tissue both types of sex-hormone are available for the direction of this differentiation. The external genitalia, in these circumstances will be predominantly, if not entirely male, for the reason that the somatic tissues being XO in constitution, will respond preferentially to the stimulus of the male sex-hormone. The internal genitalia will be a mixture of more or less well developed derivatives of both Müllerian and Wolffian ducts.

Intersexuality can thus occur in two forms in the genetic male, one being the result of an abnormality in time of differentiation of the gonads, and the other of abnormality in the mode and in the time of the differentiation of the gonads. That it should be the male that is prone to such abnormality is not surprising, for the balance in the sex-determining gene-complex is known to be less stable in the digametic (XO) than in the monogametic (XX) sex.

Of course, it may well be that these individuals are genetic females (in fact, further investigation is providing evidence which would seem to show that they are), that the differentiation of the gonads is in the order right to left, caudad pole to cephalad, and that the female-determining factors are the relatively slowly-elaborating. Baker (1925) is definitely of this opinion and has brought forward evidence which supports his view. However, it is thought fit to present the above highly speculative interpretation in order to draw the attention of other workers to the advantages of the pig as experimental material for use in this particular field of biological enquiry.

In the goat and also in the human being, judging from the descriptions of ovotestes given by different writers (e.g., Krediet, 1921) the course of gonadic differentiation is different from that which obtains in the pig, as is also the time relation in the differentiation of the structures of the accessory sexual apparatus and external genitalia. Nevertheless, with a few modifications the scheme suggested for the pig can be adapted for the interpretation of the conditions found in the human intersexual, and of the very many hermaphrodites in the mammals, fish, and amphibia.

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HUMAN TYPES

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THIS paper on human types embodies the results and records obtained by the author during investigations in America, Europe, Japan and the Philippines, and a discussion of the relation of this work to the general literature on the subject. More than 100,000 records have been tabulated by the writer. The persons measured or examined included 16,345 American Whites, 7,507 American Negroes, 5,298 Filipinos, 3,940 Japanese, 562 Chinese, 561 Spanish, 71 East Indians, and a few American Indians.

The problem of human types is one that has baffled the ages, and it is not yet in a fair way to complete solution. Many factors such as heredity, environment, isolation, dispersal, differentiation, crossing and recrossing have resulted in mosaics of peoples throughout the world. It would take too much space to try to unravel the complexities, but a word as to some of the chief transformations up to the present time may not be out of place.

The Neanderthal man of the Mousterian period in Europe was of the extreme Mesomorph, or intermediate form of man from the anatomical or morphological standpoint. Modifications of this form exist throughout Oceania and in Africa, and may be seen in Europe, as recorded in recent anthropological surveys in the small islands of Denmark (64). Throughout the Pacific area this form has been called Australoid, and in Africa occurs among the purer Negroes. It has become modified among the Yellow-Brown peoples in Asia and America where it resembles the late Paleolithic forms of Europe. The modifications of the Neanderthal may be seen in Europe in the Spy skeletons, again at Krapina, and in Moravia and Bohemia, as well as in the Aurignacian and Solutrean forms, and the later Brno, Brüx, Combe Capelle and Cro-Magnon forms (70). As the people spread to the Mediterranean and Baltic basins, with the development of the harpoon and the use of fish as food, they became smaller and slenderer so that the type changed from that of the Mesomorph to that of the Hypermorph. The pigmentation increased in the Mediterranean basin and decreased in the Baltic. Fleure (32) has traced the changing types through southern Britain, Wales and Ireland, where the face grew narrower and longer and the orbits high and narrow instead of low and broad. Around the littoral of Europe somewhat inland, and in Scandinavia, the stature remained tall whereas it became small in the south. The peoples of the interior of Europe remained more of the Mesomorph type, broad and stocky.

Certain stocks that became isolated and lived under adverse conditions were reduced to a more or less infantile form, with short arms and legs and round heads and faces. This finds its extreme manifestation among the Negrillos of Africa, the Negritos of the Pacific, and the Malays, and in a more or less modified form among the peoples of the sub-arctic

regions, as the Siberians and Lapps. This type I have called the Hypomorph.

The three types, Hypermorph or high form, Mesomorph or medium form and Hypomorph or low form, are the three outstanding generalized forms of man. Only the first two are found in Europe or among the White peoples, whereas all three types are found among the Blacks and Yellow-Browns.

The chief anthropometric characters of the three types may be given in a general way as in table 1.

It may be seen that this method of classification of man into types cuts squarely across the recognized races or groups of man, whether we take the grouping of Haddon (39) into Straight-Haired, Wavy-Haired and Wooly-Haired, or that of Hrdlička into White, Black and Yellow-Brown or almost any other classification of man that has been devised by anthropologists. The present classification into Hypomorph, Mesomorph and Hypermorph has the advantage of a large number of conformable characters, only the chief of which were grouped in table 1. It does not attempt to group into races, but only calls attention to some coördinate characters that are found together among men throughout the world.

The question arises as to whether the coördinate characters are the result of phylogeny or ontogeny; whether they are the result of evolution or of individual development. Evidence of the incoördinate conditions in evolution has been advanced by Hooten in a study of many characters of man and apes, conditions that he groups under the term asymmetrical evolution, but that might more properly be called incoördinate evolution. I called attention to similar conditions noted in the living in a previous paper (19), where the suggestion was made that characters as well as types have undergone evolution and have become exaggerated in one direction or another. Thus the nose is broad and flattened in the Black, narrow and high in the White and intermediate in the Yellow-Brown. The woolly hair of the Black and the straight hair of the Yellow-Brown are extremes, neither of which has been reached in the White. The dark skin of the Black and the light skin of the White are more extreme than the intermediate coloring of the Yellow-Brown. The glabrous Yellow-Brown

TABLE 1

Generalized characters of the three types

CHARACTER	HYPOMORPH	MESOMORPH	HYPERMORPH
Stature	Small	Medium	Tall
Sitting height	High	Medium	Low
Legs	Short, broad	Medium	Long, narrow
Arms	Short, broad	Medium	Long, narrow
Body	Round	Bulky	Wiry
Neck	Broad	Medium	Narrow
Shoulders	Broad	Medium	Narrow
Thorax	Broad	Medium	Narrow
Hips	Broad	Medium	Narrow
Nose	Short, broad	Medium	Long, narrow
Ears	Short, broad	Medium	Long, narrow
Hands and feet	Short, broad	Medium	Long, narrow

and the hirsute White are more extreme than the intermediate hairiness of the Black. The ear type of the White is between that of the Black and of the Yellow-Brown. The large brain of the White and the small brain of the Black are more extreme than the brain of the Yellow-Brown. Similarly we might point out that the legs of the Negro are the longest and those of the Yellow-Brown the shortest, with the White in between; the arms, hands, feet, trunk, and many other parts of the body may be differentiated in like manner. These variables are but an illustration of oscillation in evolution which produces different results upon various characters under different conditions.

The result is that neither the White, nor the Black nor the Yellow-Brown is extreme nor is any one of them intermediate, in all of the characters mentioned. Continental areas have not produced homogeneous results. The White of Europe, the Black of Africa and the Yellow-Brown of Asia are not uniform in their characters in relation to each other. On the other hand the Hypomorph, Mesomorph and Hypermorph are uniform regardless of race or continental area. Other factors have been more potent than these in their formation. The Hypermorph has been found more extreme in its characters near the sea, as about the Mediterranean and Baltic and in Britain and Japan; the Mesomorph has remained more marked in character in the interior of continental areas; and the Hypomorph has been most extremely developed in the tropics and arctic regions under adverse living conditions.

The distribution of these types has been treated at some length in papers that have appeared during the past three years in the *American Journal of Anatomy*, (17), (18), (19). Their characters have also been presented in a general way with descriptions of their movements, and of their development and evolution. The types will now be illustrated, and their exact measurements as found in typical persons will be given, with some discussion in detail as to the composition of the types. First, outline drawings will be given of the types among the Blacks and Yellow-Browns; then photographs will be used for the Whites. The outline drawings were made by projection from actual photographs, and in order to show the characteristic differences few lines were made. The outlines bring out the desired characters better than photographs, and the differences are more easily and clearly seen because no distracting or extraneous structures are shown.

1. TYPES OF THE BLACK RACE

Figures 1, 2 and 3 represent three American Negroes in side view and figures 4, 5 and 6 three Negritos of the Philippines in front view. Figures 1 and 4 are Hypomorph, figures 2 and 5 are Mesomorph, and figures 3 and 6 are Hypermorph.

The Hypomorph (17) has a broad, flattened nose that is button like, as in the infant, depressed at the root and along the bridge and over the ridge; eyes that are wide apart and nearly closed, with a tendency toward the Mongolian Fold; and thick, everted lips. The ears are small, rounded and semi-bowl shaped. The face and cranium are rounded and somewhat flattened in front.

The Mesomorph (17) has a broad, pyramidal nose, that is somewhat flattened but is not so much depressed as that of the Hypomorph at the root and along the bridge and over the ridge; eyes that are not so far apart, with a slight tendency toward the Mongolian

Fold; and a large mouth without the thick everted lips. The ears are large and not so bowl-shaped as in the Hypomorph, and the cranium and face are large and oval, without so much flattening in front.

Figures 7, 8 and 9 illustrate the proportions of the extremities in relation to the remainder of the body. Figure 7 is the Hypermorph, figure 8 the Mesomorph and figure 9 the Hypomorph. These are photographs of three Negritos of the Philippines. The legs of the Hypomorph are relatively to stature or to sitting height very short, and the trunk is very long. The arms are also relatively short but not so much so as the legs. The hands and fingers are broad and short, and other characters of the Hypo-

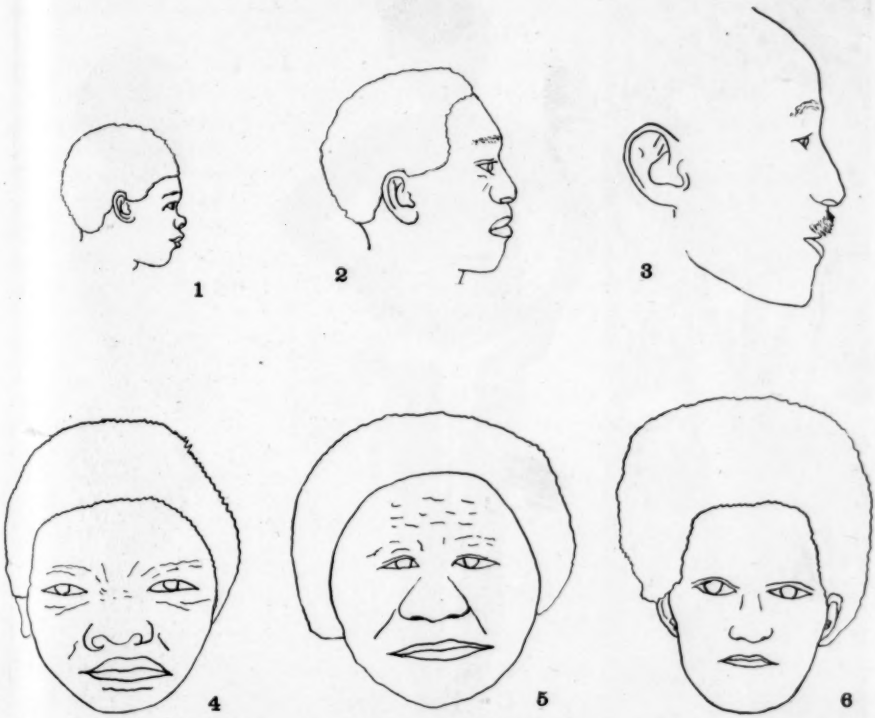


FIG. 1. AN AMERICAN NEGRO OF THE HYPOMORPH TYPE. FIG. 2. AN AMERICAN NEGRO OF THE MESOMORPH TYPE. FIG. 3. AN AMERICAN NEGRO MIXED WITH WHITE OF THE HYPERMORPH TYPE. FIG. 4. A FILIPINO NEGRITO OF THE HYPOMORPH TYPE. FIG. 5. A FILIPINO NEGRITO OF THE MESOMORPH TYPE. FIG. 6. A FILIPINO NEGRITO OF THE HYPERMORPH TYPE.

The Hypermorph (17) has a narrow, long, high nose; eyes that are close together and wide open; a small mouth with thin lips; and thin ears with slender helix and everted tragus and antitragus. The cranium and face are long and narrow.

morph may be seen. The legs of the Hypermorph are relatively to stature or to sitting height very long, and the trunk is very short. The arms are relatively long but not so much so as the legs. The hands and fingers are long and narrow and other characters of the Hypermorph may be seen. The Mesomorph is in between the Hypomorph and Hypermorph.

The Black Hypermorph seems to be the result of mixture with some other stock; the typical ones are invariably of mixed stock in America, and probably also in Africa, therefore they may be left out in presenting the measurements of

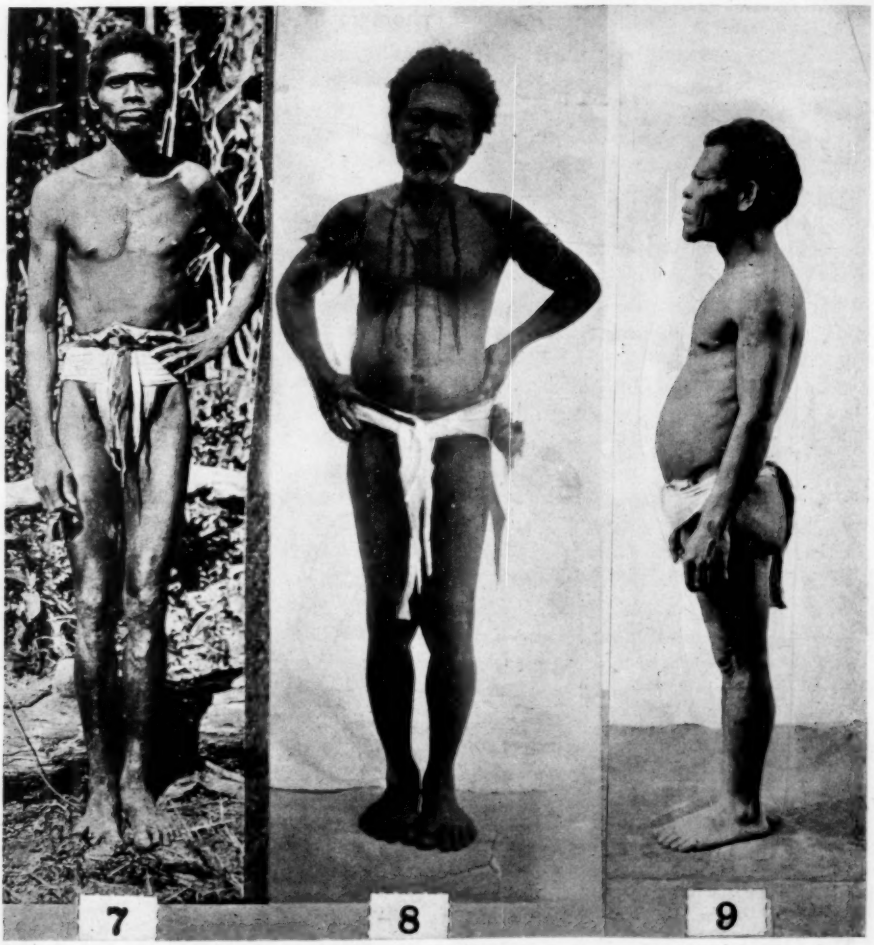


FIG. 7. A FILIPINO NEGRITO OF THE HYPERMORPH TYPE. FIG. 8. A FILIPINO NEGRITO OF THE MESOMORPH TYPE. FIG. 9. A FILIPINO NEGRITO OF THE HYPOMORPH TYPE

typical persons of the Black Race. Measurements of a typical male and female Hypomorph and Mesomorph of the Black Race are given in table 2.

TABLE 2

Actual measurements of typical Hypomorph and Mesomorph persons of the Black Race

	HYPOMORPH		MESOMORPH	
	Male	Femal	Male	Female
Character:				
Stature	151.0	145.0	167.1	156.8
Sitting height	81.5	77.1	84.2	79.0
Leg length	69.7	67.9	82.9	77.8
Arm length	71.2	67.2	76.0	70.5
Acromion height	121.0	116.7	136.0	128.0
Head length	18.0	17.8	18.8	17.8
Head breadth	14.8	14.3	14.1	13.8
Nose length	4.3	4.2	4.65	4.0
Nose breadth	4.5	4.3	4.8	3.7
Ear length	5.4	5.2	5.9	5.5
Ear breadth	3.6	3.1	3.7	3.3
Index:				
Sitting height / Stature	54.0	53.2	50.4	50.5
Sitting height / Leg length	117.0	113.5	102.0	101.0
Sitting height / Arm length	114.5	114.5	111.0	112.0
Head breadth / Head length	82.0	80.0	75.0	79.0
Nose breadth / Nose length	105.0	105.0	103.0	93.6
Ear breadth / Ear length	66.5	59.8	63.0	60.0

The measurements and indices speak for themselves and show the obvious differences between the Hypomorph and Mesomorph. The stature of the Hypomorph is less than that of the Mesomorph, and as the sitting height of the two is not greatly different, the chief difference is in the leg length. The arm length shows less difference than the sitting height and much less difference than the leg length. This comes out clearly in the indices. The sitting height divided by the stature shows a difference of about 5 per cent between the Hypomorph and the Mesomorph; the sitting height divided by the leg length shows a difference of about 12 per cent; and the sitting height divided by the arm length shows a difference of about 3 per cent. The index, of the sitting height divided by the stature, of the Mesomorph is a true Negro index whereas that of the Hypomorph is a Negrillo index. The same may be said of the cephalic index, or the head breadth divided by the head length, and of the nasal index, or the nose breadth divided by the nose length. This means that the True Negro is a Mesomorph and the Negrillo is a Hypomorph.

A great many other characters might be selected that would show as well as these the differences between the Hypomorph and Mesomorph but these will suffice. It must not be assumed that each person among the Blacks will be exactly like the examples given because this is not the truth. There are so many variants that only the extreme forms may be readily allocated to one group or the other. The great mass of the Blacks, in fact, will be found to be different from either the Hypomorph or the Mesomorph because these are the extremes. It may be possible to show that each person is like a Hypomorph or like a Mesomorph although not strictly one or the other. This will be brought out later in dealing with the Whites where a more intricate and detailed analysis of the types becomes possible. The Whites are more heterogeneous because of greater mixtures yet they have less distant extremes because of more homogeneous environment.

We may now turn to a consideration of the types of the Yellow-Browns.

II. TYPES OF THE YELLOW-BROWN RACE

The Blacks and the Yellow-Browns have come together in India and Oceania as well as in southeastern Asia, therefore the Malays, Melanesians and Polynesians should be treated as mixtures of those two races with the addition of some Whites from near the Mediterranean, called in India, Pre-Dravidians, and other Whites from the north, called Indo-Europeans. It would take too much time and space to unravel the complexities of such a conglomerate even were it possible. A few characteristic outlines of the face will be given, with a later analysis of a Malay group in averages.

Figure 10 shows a Hypomorph Filipino Negrito; figure 11, a Mesomorph Melanesian; figure 12, a Hypermorph Polynesian; figure 13, a Hypomorph Chinese; figure 14, a Mesomorph Chinese; and figure 15, a Hypermorph Japanese. These do not represent the only types of the groups to which they belong, but are the most characteristic types of the groups. The Negritos are more Hypomorph, the Melanesians are more Mesomorph and the Polynesians are more Hypermorph; whereas the Chinese are both Hypomorph and Mesomorph, and the Japanese are Hypermorph among the upper classes although both Hypomorph and Mesomorph among the lower classes.

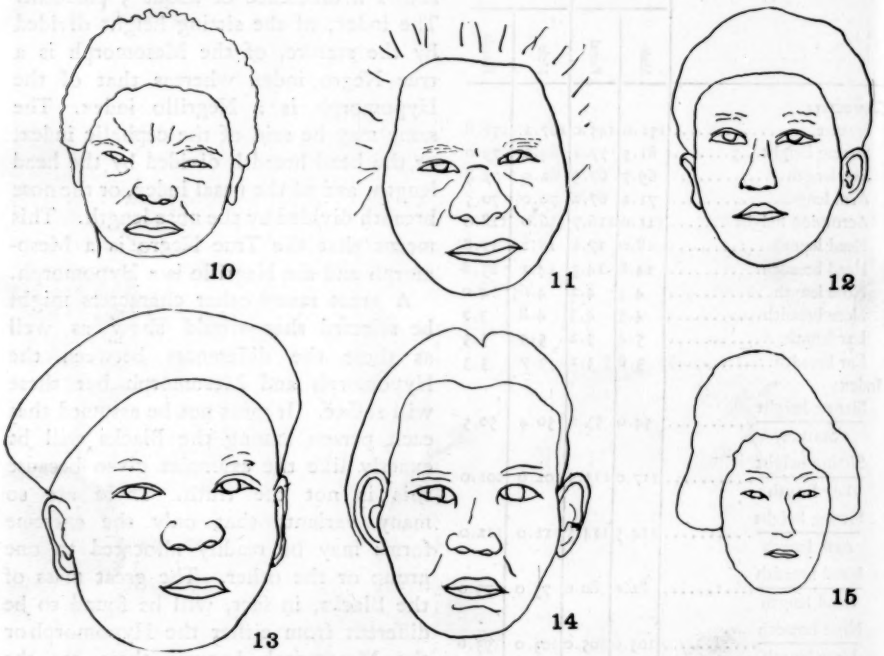


FIG. 10. A FILIPINO NEGRITO OF THE HYPOMORPH TYPE. FIG. 11. A MELANESIAN OF THE MESOMORPH TYPE. FIG. 12. A POLYNESIAN OF THE HYPERMORPH TYPE. FIG. 13. A CHINESE OF THE HYPOMORPH TYPE. FIG. 14. A CHINESE OF THE MESOMORPH TYPE. FIG. 15. A JAPANESE OF THE HYPERMORPH TYPE.

The Negrito and the Melanesian are like the Hypomorph and Mesomorph Blacks, which they are in fact, and the Polynesian is like the Hypermorph of the Whites. The Chinese and Japanese are Yellow-Browns. The Mesomorph Chinese is like the Hypermorph Black, and the Hypermorph Japanese is like the Extreme Hypermorph White. Further description of the types is unnecessary if the reader will refer to the descriptions already given for the types among the Blacks.

A great difference was found between the official classes and the laboring classes when examining the Japanese in 1907 and 1910. The percentage proportions of the types are given in table 3.

TABLE 3
The proportions of the types in Japan

CLASS	HYPOMORPH	MESOMORPH	HYPERMORPH	NUMBER
Official, male	3.1	26.5	70.4	256
Laborer, male	28.1	58.3	13.6	3,812
Both, female	27.6	45.5	26.9	442

The difference is so great and so striking that the two classes seem almost to be different races, although both are Yellow-Brown. A photograph is presented in figure 16 of a lady of the upper class who is a true Oriental although much like many Europeans of the Mediterranean stock, of Spanish or even of English extraction. The inference is that insular life during a considerable period of time has produced in the Orient similar types to those of the Occident under similar conditions. As Fleure (32) has found that the south Britons have become slenderer, so we may presume that the Japanese have done the same, especially in the higher classes.

FIG. 16. A JAPANESE WOMAN OF THE RULING FAMILY, OF THE EXTREME HYPERMORPH TYPE
From World Wide Photos

We may now present the actual measurements of typical representatives of the Hypomorph, Mesomorph, and Hypermorph Yellow-Browns (table 4).

The differences between the types are obvious from this table of measurements, and verify the descriptive differences already given. The stature, head breadth and leg length are especially characteristic as are also all of the indices. Attention is directed to certain differences between the types of the Black Race and the Yellow-Brown. The head breadth, nose length and ear length of the Yellow-Brown types are uniformly greater than those of the Black types. These are racial differences that are not obscured by the type differences; neither does one set of characters vitiate the other. Both are obvious.

The Blacks have the shortest ears and the broadest noses in the world, and the Yellow-Browns have the longest ears and the broadest heads in the world. The Yellow-Browns have a high cephalic index and the Blacks a low one. On the other hand the Hypomorph has great head breadth, the Mesomorph less and the Hypermorph least; the Hypomorph has a high cephalic index, the Meso-

TABLE 4

Actual measurements of typical Hypomorph, Mesomorph and Hypermorph persons of the Yellow-Brown Race

	HYPOMORPH		MESOMORPH		HYPERMORPH	
	Male	Female	Male	Female	Male	Female
Character:						
Stature	149.8	142.1	168.4	152.2	170.7	155.8
Sitting height	83.0	75.5	88.1	80.5	88.8	79.0
Leg length	66.8	66.6	80.3	71.7	82.5	76.8
Arm length	67.3	65.7	79.0	67.8	80.5	70.2
Acromion height	120.3	115.2	138.0	122.8	138.7	128.6
Head length	17.2	16.3	18.3	17.2	18.2	18.0
Head breadth	15.3	14.2	15.6	14.6	14.3	14.1
Head height	13.0			12.3	12.4	12.3
Nose length	4.6	3.4	4.7	4.6	4.4	4.9
Nose breadth	4.1	3.9	4.2	4.0	3.6	3.8
Ear length	6.3	5.9	6.7	6.6	6.3	6.3
Ear breadth	3.6	3.6	3.8	3.6	3.6	3.2
Index:						
$\frac{\text{Sitting height}}{\text{Stature}}$	55.4	53.1	52.2	52.8	51.6	50.7
$\frac{\text{Sitting height}}{\text{Leg length}}$	124.0	113.2	109.5	112.3	107.0	102.4
$\frac{\text{Sitting height}}{\text{Arm length}}$	123.6	115.0	111.4	118.5	109.5	112.5
$\frac{\text{Head breadth}}{\text{Head length}}$	89.0	87.1	85.3	85.0	78.5	78.0
$\frac{\text{Nose breadth}}{\text{Nose length}}$	89.1	114.7	89.0	87.0	81.8	77.5
$\frac{\text{Ear breadth}}{\text{Ear length}}$	57.2	61.0	56.8	54.6	60.2	50.7

morph less and the Hypermorph least; and the Hypomorph has a high nasal index, the Mesomorph less and the Hypermorph least. The ear index is not so good a differentiator of type as the other characters, or as the form of the ear from the descriptive point of view. The descriptive characters of the ear (10) have been used by me more than any other single character, although the nose is equally characteristic, but I have described the ear and nose types in other publications (7) (8) (11) (12) (13) (17), therefore it is not necessary to repeat the descriptions here.

TABLE 5

Number of Filipinos in each sex, type and age group

TYPE	AGE												
	− 6	− 8	− 10	− 12	− 14	− 16	− 18	− 20	− 25	− 30	− 40	− 50	− 60+
Male													
Hypomorph	4	1	2	6	9	14	7	6	5	4	3	2	1
Mesomorph	4	8	11	10	19	73	189	117	53	27	22	19	17
Hypermorph	6	2	6	9	10	23	39	26	13	9	16	4	6
Female													
Hypomorph		2	1		2	6	9	7	3	2	3	2	
Mesomorph			2	7	8	21	20	13	8	7	3	11	5
Hypermorph		1		5	8	7	18	2	4	2	8	6	3

Tables 6 and 7 illustrate by averages the actual measurements of 1,008 Filipinos between the ages of 5 and 80 years. Table 5 shows the number at each age and in each sex.

Three groups of Filipinos are included in table 5. Those under 12 years are from the schools in Manila, residents of that city and largely of the littoral or coast Malays, Neo-Malays. Those between 14 and 25 are students of the Normal and Trade schools in Manila, and from all parts of the Philippines. They are also Neo-Malays, but have a large number of Chinese and Spanish Mestizos among them. Some of those between the ages of 14 and 25 are from Taytay, where all the remainder between the ages of 25 and 80 reside. These are the purest Malays, although they may have a trace of East Indian and Chinese among them. In spite of this conglomerate and in spite of the small numbers at certain ages the tables show fairly uniform differences between the types. The entire group is a fair representation of the Yellow-Brown Race, although there are no American Indians among them. The stock from which the American Indians came is well represented, as also are related stocks.

In tables 6 and 7 the male and female statures are shown for the three types. The Hypomorph is of lower stature at all ages than either the Mesomorph or the Hypermorph, and the latter two have nearly the same stature although the stature of the Mesomorph is usually less than that of the Hypermorph. The high stature at the age of 20 years is due to the large number of Mestizo students. The stature after that age is smaller because only the Malays of Taytay are included. The

averages of the females are more irregular than those of the males because of fewer females at each age.

the types as those of the stature, although not so clearly. The female is particularly irregular and in the early years the

TABLE 6

Average measurements of Filipinos and Whites (males) between the ages of 5 and 80 years

Dimensions are in centimeters

	AGE													
	– 6	– 8	– 10	– 12	– 14	– 16	– 18	– 20	– 25	– 30	– 40	– 50	– 60	– 70
Stature														
Filipino hypomorph	—	104	115	131	140	143	152	157	152	151	152	152		152
Filipino mesomorph	110	115	123	134	149	159	164	168	167	159	159	159	162	—
Filipino hypermorph	106	121	126	137	138	158	168	164	166	161	163	162	166	160
White mesomorph	115	119	131	140	150	—	166	171	173	173	171	172	170	—
White hypermorph	120	124	134	143	155	—	175	176	177	178	175	176	176	174
Sitting height														
Filipino hypomorph	58	59	61	68	70	78	81	83	82	82	81	82	81	78
Filipino mesomorph	59	62	64	68	76	82	84	84	85	84	84	85	84	—
Filipino hypermorph	56	61	65	70	77	82	85	86	86	84	87	86	86	81
White mesomorph	62	63	68	72	76	—	89	91	93	93	93	93	93	91
White hypermorph	62	64	68	73	78	91	90	93	94	94	93	94	94	92
Leg length														
Filipino hypomorph	49	45	51	63	71	73	71	73	71	70	70	71		
Filipino mesomorph	—	55	58	64	73	77	78	79	78	75	76	75	76	
Filipino hypermorph	—	54	61	66	76	79	81	78	78	75	77	80	78	77
White mesomorph	54	56	64	69	73	—	79	83	84	84	81	81	79	—
White hypermorph	57	61	67	71	77	—	—	86	85	85	85	85	84	81
Leg index														
Filipino hypomorph	119	116	114	108	102	105	114	113	113	121	113	116		
Filipino mesomorph	117	113	109	108	105	106	107	107	109	113	112	115	114	111
Filipino hypermorph	115	110	105	107	100	105	107	109	109	113	114	112	110	—
White mesomorph	118	115	108	106	106	—	—	108	110	112	114	115	116	—
White hypermorph	106	106	105	102	103	—	—	104	106	108	107	110	111	—
Hand length														
Filipino hypomorph						148	178	172	168	163	164	163	157	
Filipino mesomorph							168	178	178	178	177	179	180	181
Filipino hypermorph						173	166	188	184	178	185	184	183	178
White mesomorph														
White hypermorph														

The averages of the male and female sitting height as shown in tables 6 and 7 illustrate the same differences between

averages almost coincide. The differences are clearer in the males. Here, as in the stature, the Hypomorph has a lower

sitting height at practically all ages than the Mesomorph and Hypermorph, and the latter two are close together.

types, although in the female, as usual, the difference is not so clear as in the male. The sexual factor in the female

TABLE 7

Average measurements of Filipinos and Whites (females) between the ages of 5 and 70

Dimensions in centimeters

	AGE													
	– 6	– 8	– 10	– 12	– 14	– 16	– 18	– 20	– 25	– 30	– 40	– 50	– 60	– 70
Stature														
Filipino hypomorph	114	121	125	137	145	145	151	150	150	145	145	140	–	
Filipino mesomorph	–	–	–	140	148	152	154	154	154	147	149	144	144	144
Filipino hypermorph	–	116	125	140	149	154	154	156	151	151	150	150	146	
White mesomorph	117	121	130	140	150	156	–	161	163	160	160	160	160	160
White hypermorph	118	123	132	146	156	160	163	163	163	163	164	165	163	161
Sitting height														
Filipino hypomorph	–	61	66	73	78	78	81	81	81	78	78	77		
Filipino mesomorph	–	–	–	73	75	78	79	80	82	79	79	78	76	76
Filipino hypermorph	–	59	65	72	76	81	81	84	80	81	80	79	79	–
White mesomorph	61	62	67	75	79	81	–	–	87	86	88	86	87	85
White hypermorph	63	66	69	75	81	84	–	–	86	86	86	87	87	84
Leg length														
Filipino hypomorph	–	55	57	65	70	67	70	69	70	69	68	67	–	–
Filipino mesomorph	–	–	–	67	73	73	74	73	73	68	70	70	70	68
Filipino hypermorph	–	60	63	67	71	72	73	72	72	72	72	72	65	–
White mesomorph	53	57	62	68	73	73	–	–	76	76	73	73	72	–
White hypermorph	54	59	64	71	76	78	–	–	77	77	79	79	79	78
Leg index														
Filipino hypomorph	–	113	112	111	110	113	112	114	113	114	111	112	112	
Filipino mesomorph	117	114	111	108	103	107	107	110	112	114	112	112	111	
Filipino hypermorph	–	–	–	107	105	111	109	116	114	116				
White mesomorph	117	109	108	105	107	106	–	–	117	118	122	117	118	116
White hypermorph	118	112	104	105	106	105	–	–	111	107	111	111	111	111
Hand length														
Filipino hypomorph							172	161	157	145	166	160		
Filipino mesomorph									155	162	162	162	161	158
Filipino hypermorph									168	178	158	168	158	168

The averages of the male and female leg length as shown in tables 6 and 7 illustrate more clearly than those of sitting height the difference between the

may have something to do with the irregularity of the data, although the small number of persons may also be responsible. The greatest difference so far noted is in

the short legs of the Hypomorph in relation to the leg length in the other two types. This is one of the chief differences noted between the types.

The averages of the male and female leg index, or the sitting height divided by the leg length, as given in tables 6 and 7 show differences between the Hypomorph and Hypermorph, with the Mesomorph in between, during the earlier years especially; but there is some irregularity in the adult and preadult stages. These averages fall as the legs grow rapidly and rise as the sitting height grows rapidly. The Hypomorph average is above the others in the male and also to some extent in the female.

The averages of the male and female hand length as shown in tables 6 and 7 illustrate the differences between the three types in this respect. The Hypomorph has a short hand, the Mesomorph is intermediate and the hand of the Hypermorph is long. The hand of the Hypomorph is also broad, that of the Mesomorph is intermediate, and the hand of the Hypermorph is narrow. The Chinese have long narrow hands, therefore the index of the hand, the width divided by the length, would be Hypermorph. It is about 40 in the Chinese; whereas it is about 42.5 in the American White Hypermorph and about 45 in the American White Mesomorph. The hand breadth of the Filipinos was not measured, but from observation the hand index of the Hypomorph Filipino is between 45 and 50.

Tables of averages of the same kind as those given have been made for such characters as the head height, head breadth, head length, cephalic index, mean head height index, head height-head length and head height-head breadth indices, nose length, nose breadth, nasal index, ear length, ear breadth, ear index, upper arm length, lower arm length, brachial index, hand length, hand breadth, upper leg, lower leg, crural index, intermembral index, leg-sitting height index, arm-sitting height index, and others. In all of these the three types may be separated more or less. When it is considered that the types were determined chiefly by the careful inspection of the ear and nose form, it will be understood that the types are anthropometric entities as well as morphologic forms. The measurements and curves corroborate the evidence of the eye. It is of great interest and importance that the type holds together so well. In rare individuals there is a mosaic. Sometimes the head will be Hypomorph and the arms and legs Hypermorph, again the head will be Hypermorph and the arms and legs Hypomorph. Then again the ears will be of one type and the nose and body of another, and so on. There are also blends and fusions of many degrees, making an almost interminable variety of forms. The Hypomorph and Hypermorph are the extremes, and they are selected with more care than the Mesomorph, because among the Mesomorphs are included mixed and mosaic forms.

III. TYPES OF THE WHITE RACE

Aristotle (50) taught that "The first principles are fire, air, water and earth, for from them are formed all living things and the productions of the earth: they are therefore called elements," but Aristotle also said "In general it is silly to rely on a single sign: you will have more reason for confidence in your conclusions when you find several signs all pointing the same way." Hippocrates (1) used the temperaments throughout his practice, and considered the different characters of the races of man as the result of

environment. The strongest natural causes of variability in man were the seasons, then the country, and the waters, according to Hippocrates. Both he and Galen taught that the different kinds of moisture in man's body, phlegm, blood, choler and melancholy, as they predominate, determine the temper of the mind. "An exact balance of the four humors makes a justly constituted man, and allows for the undisturbed processes of digestion and assimilation." The School of Salerno (40) which flourished during the crusades was a Mecca for great physicians as well as celebrated patients and taught the four temperaments of Hippocrates. Albrecht Dürer depicts the four temperaments in the form of four apostles, and they have been variously represented by other great artists.

The temperaments as depicted by Albrecht Dürer, and as taught at the School of Salerno, based upon the four elements of Aristotle, air, earth, fire, and water and upon the four humors of Hippocrates blood, black bile, yellow bile and phlegm, and known as the sanguine, melancholic, choleric, and phlegmatic, may not be generally accepted; and the rheumatic, catarrhal, phthisical and plethoric diatheses may have a greater significance, but doubtless all of these four categories in relation to man refer to four races that may have been recognized early in the history of Europe. The fiery Spaniard or other Mediterranean people may represent the choleric temperament, the Nordic the sanguine, the Celts were phlegmatic, "fair and white," while the Alpines were both "swart and colly," dark and melancholy. The races may have been more distinct in the time of Hippocrates than at present, because at present mosaics and blends are numerous and even the four races are not distinct. One may select the four races from a large group, but they will show great variability.

An investigation of students was made at the University of Michigan in 1906, and this was followed by a similar study at Tulane University in 1913, and since then at the University of Virginia. Nearly 2,000 students were measured and examined. An attempt was made to select from these the ones that conformed to the four races, with the results as given in table 8.

The approximate proportions of different nationalities in the ancestry from casual memory of the students was: English 37 per cent, German 11 per cent, Scotch 10 per cent, Dutch 8 per cent, French 5 per cent, and the remainder scattering over many nations. The class standing in the Freshman year was: Celt about 85, and Alpine, Nordic and Mediterranean about 75.

The important findings from this study are that only about 60 per cent of all the students could be considered as belonging to the four races, and there is great variability so that each group is hardly an entity, but a conglomerate of variables. The four races represent only two morphologic forms because the Nordic and Mediterranean are very much alike except in pigmentation, as are the Celt and Alpine. The remaining 40 per cent of the students present so many mixtures, blends and mosaics that it was almost impossible to classify them with the four races, but they could be fairly well grouped into the two morphologic forms.

Measurements of school children and Old Americans (49) were made later,—the Old Americans during the past few years, —and averages from these measurements may be seen in tables 6 and 7. Each person was grouped as a Mesomorph or as a Hypermorph, although a more striking difference might have been revealed

if they had been grouped as the Filipinos were, into two, small, extreme groups and a large intermediate one. Two sets of people were utilized for the tables,—about 1,500 school children of Ann Arbor, Michigan, and about 2,000 Old Americans (49) recently measured in Virginia. Only the British-American children of Ann Arbor, and only the most recently examined Old Americans of Virginia were used. The two groups are fairly comparable although only in the Old Americans was the ancestry for two generations obtained.

The stature as given in tables 6 and 7 is greater at all ages in the Hypermorph than in the Mesomorph, and the difference is greater in the adult than in the children, and greater in the male than in the female. The stature of the American Whites is greater than that of the Filipinos, although the stature of the Hypermorph Filipino comes close to that of the Mesomorph White.

The sitting height (tables 6 and 7) is in general greater in the Hypermorph than in the Mesomorph but the difference is not so great as in the stature. The difference between the Filipino and American White is slight except in the adult.

The leg length (tables 6 and 7) is greater in the Hypermorph than in the Mesomorph, and the difference is considerable in both sexes at all ages.

The leg length index (tables 6 and 7) is extremely different in the two types especially in the adult. This index shows that the hypermorph has long legs and the Mesomorph short ones with the sitting height reversed, the Hypermorph short and the Mesomorph long.

More than 40 charts have been prepared of measurements and indices of the vari-

TABLE 8

Characters of the four European races

CHARACTERS	NORDIC		MEDITERRANEAN		ALPINE		CELT	
	Average	Variability	Average	Variability	Average	Variability	Average	Variability
Male								
Body:								
Weight	66.3K	±7.3	63.1	±7.2	63.1	±7.2	65.9	±6.7
Per cent pigment	35.4	±12.7	87.1	±12.4	84.5	±9.9	37.1	±12.5
Stature	174.4	±5.4	170.8	±5.8	169.4	±5.0	174.6	±3.1
Chest circumference	88.0	±5.4	86.0	±5.2	87.4	±5.4	87.8	±4.9
Head:								
Length	19.9	±0.6	19.8	±0.7	19.2	±0.7	19.2	±0.7
Breadth	15.5	±0.4	15.5	±0.4	16.0	±0.5	16.1	±0.5
Cephalic index	76.5	±2.5	76.8	±2.2	81.4	±2.3	83.6	±2.1
Female								
Body:								
Weight	53.4		52.4		47.8		53.0	
Per cent pigment	32.8		87.0		91.0		25.0	
Stature	163.0		158.8		157.0		161.0	
Chest circumference	78.5		75.0		73.7		79.0	

More than 40 charts have been prepared of measurements and indices of the vari-

ous parts of the body, and they all show differences between the Hypermorph and Mesomorph, some of which have already been given in this paper. Some of the differences are presented in table 9 as they appear in typical individuals.

TABLE 9

Actual measurements of typical Hypermorph and Mesomorph persons of the White Race

	HYPERMORPH		MESOMORPH	
	Male	Female	Male	Female
Character:				
Stature	172.1	166.6	180.0	163.3
Sitting height	89.8	87.6	95.7	88.6
Leg length	82.3	79.0	84.3	74.7
Arm length	80.1	73.1	78.3	69.7
Acromion height	143.5	141.0	150.8	136.1
Head length	19.5	19.5	20.0	19.7
Head breadth	15.1	13.6	14.8	14.3
Head height	13.4	13.5	13.3	14.1
Hand length	20.5	17.7	19.5	17.1
Hand breadth	8.5	7.8	9.1	7.9
Nose length	5.9	5.7	5.3	4.9
Nose breadth	3.3	3.0	4.1	3.7
Ear length	6.1	6.0	7.0	6.3
Ear breadth	3.6	3.6	4.4	3.6
Indices:				
Sitting height / Stature	52.0	52.5	53.1	54.3
Sitting height / Leg length	109.0	110.5	114.0	118.0
Sitting height / Arm length	112.0	119.5	122.0	127.0
Head breadth / Head length	77.5	69.8	74.0	72.6
Hand breadth / Hand length	42.3	44.0	46.7	46.2
Nose breadth / Nose length	55.9	52.5	77.3	75.5
Ear breadth / Ear length	59.0	60.0	63.0	60.3

The characters show the differences between the types except for the head and ear. The cephalic and ear indices are the least reliable of all characters in the differentiation of types. The nasal index is probably the best indicator of type. It is to be noted that the Hypermorph male is smaller than the Mesomorph. This is because an extreme Hypermorph was selected. The extreme Hypermorph is more slender than the normal Hypermorph and is also smaller, and the stature is much less in the most extreme cases.

Illustrations of the Hypermorph type are presented in figures 17, 18, 21, 22, 27 and 28, and of the Mesomorph type in figures 19, 20, 23, 24, 25, and 26. The differences that have already been described are obvious.

There is a pathological form that has been called Mongolian Idiot or Mongol, a better term for which would be Mongoloid Dwarf, which occurs in all of the three races, White, Black and Yellow-Brown, and has some of the characteristics of the Hypomorph. This type is illustrated in figures 29 and 30. Crookshank (26) has tried to prove for them inheritance from Mongolians who came into Europe at an earlier period. It is possible that it may be a form that is being eliminated by a lethal factor. Mongoloid Dwarfs usually die young, are extremely susceptible to acute infections, and all the tissues seem to be defective and deficient. A table (table 10) of some of the characters of the Mongoloid Dwarf is given to show that they are Hypomorph.

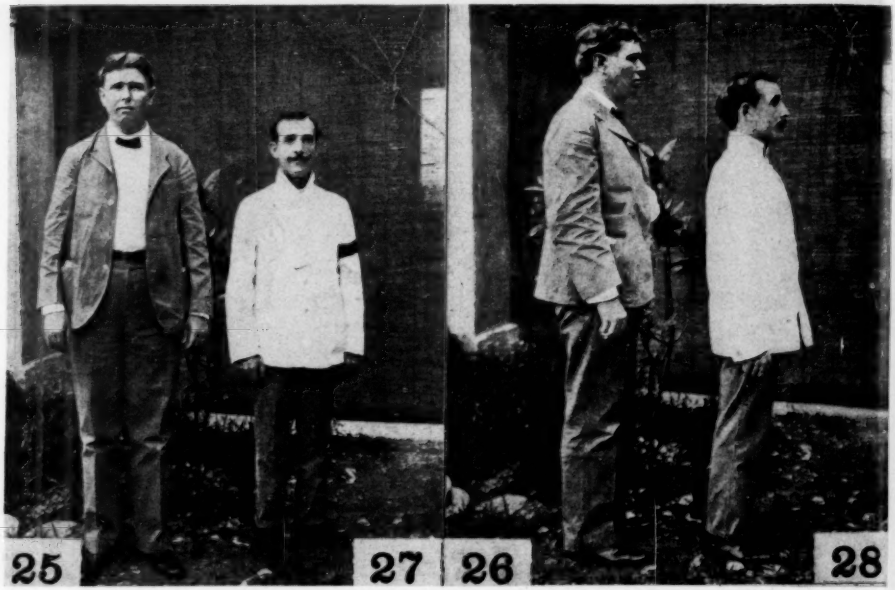
IV. DISCUSSION

Human types may be discussed under three heads, racial types, morphologic or anatomic types and physiologic types.

The definition of a Race has been conceived in divers ways, at different times, by various men. That of de Quatrefages (29b) is one of the oldest and best.

FIG. 17. AN AMERICAN WOMAN OF BRITISH-FRENCH EXTRACTION OF THE HYPERMORPH TYPE. FIG. 18. SIDE VIEW OF THE SAME. FIG. 19. AN AMERICAN WOMAN OF BRITISH-DUTCH EXTRACTION OF THE MESOMORPH TYPE. FIG. 20. SIDE VIEW OF THE SAME

FIG. 21. AN AMERICAN MAN OF THE HYPERMORPH TYPE. FIG. 22. FRONT VIEW OF THE SAME. FIG. 23. AN AMERICAN WOMAN OF THE MESOMORPH TYPE. FIG. 24. SIDE VIEW OF THE SAME



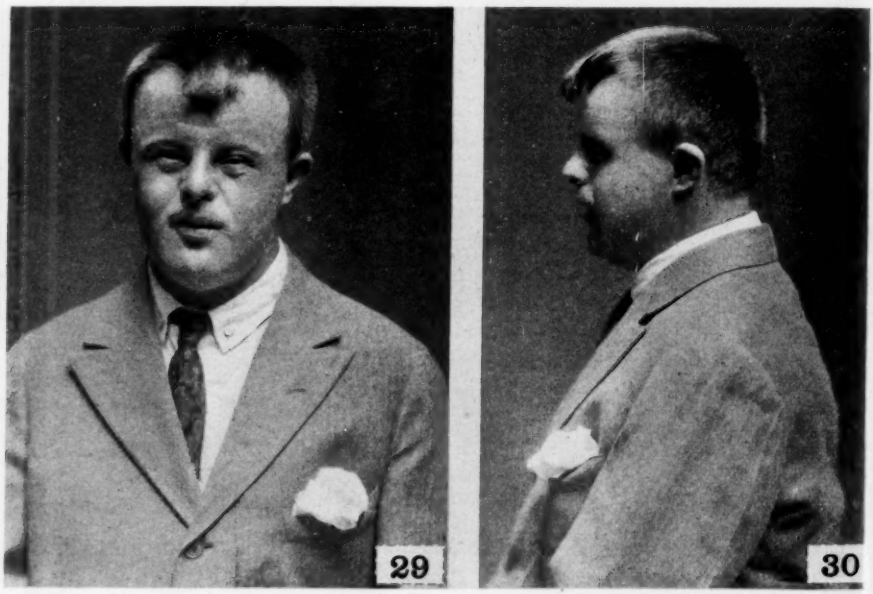


FIG. 25. FRONT VIEW OF AN AMERICAN MAN OF BRITISH ANCESTRY OF THE MESOMORPH TYPE. FIG. 26. SIDE VIEW OF THE SAME. FIG. 27. FRONT VIEW OF A SPANIARD OF THE EXTREME HYPERMORPH TYPE. FIG. 28. SIDE VIEW OF THE SAME. FIG. 29. FRONT VIEW OF A MONGOLOID DWARF OF THE WHITE RACE. FIG. 30. SIDE VIEW OF THE SAME.

TABLE 10

Measurements of a typical Mongoloid Dwarf woman, aged 25, and man, aged 28

	FEMALE	MALE
Character:		
Stature	139.9	146.3
Sitting height	81.1	83.6
Leg length	58.8	62.7
Arm length	58.0	59.3
Acromion height	116.8	120.3
Head length	16.7	16.8
Head breadth	14.3	15.2
Head height	12.7	13.3
Nose length	4.7	4.7
Nose breadth	3.5	3.4
Ear length	4.7	6.0
Ear breadth	3.3	3.4
Indices:		
Sitting height / Stature	58.0	57.1
Sitting height / Leg length	137.8	133.5
Sitting height / Arm length	139.2	141.0
Head breadth / Head length	85.6	97.8
Nose breadth / Nose length	74.6	72.3
Ear breadth / Ear length	70.4	58.3

A *Species* is a group of individuals, more or less resembling each other, that are descended, or that ought to be regarded as having descended, from a single primitive pair by a natural and uninterrupted succession of families.

A *Variety* is an individual or group of individuals pertaining to the same sexual generation, that is distinguished from other representatives of the same species by several exceptional characters.

A *Race* is a great group of people who have had the same origin; who have spread over a large area of the earth; and who resemble one another in a great many stable characters.

A *Race* is therefore only part of a broken up *Species*.

Hooton (44) has within the year defined a Race as "a great division of mankind, the members of which, though individually varying, are characterized as a group by a certain combination of morphological and metrical features, principally non-adaptive, which have been derived from their common descent." He then gives a list of characters that are principally non-adaptive. Some of these are subject to sexual selection and should be omitted. Other characters that are modifiable and may be remodified might be added. Then we would have as the best differential characters the following: Hair form, sutural patterns, postglenoid tubercle, pharyngeal fossa or tubercle, form of incisor teeth, form of the vertebral border of the scapula, supracondyloid process or foramen, the crural and brachial indices, bowing of the radius and ulna, nasal index, hard palate, height of head, volume of brain, proportions of thorax, relative length and angle of the heel bone, and size and development of the calf muscles. To these might be added the form of the external ear, and of the nose, and the hand index, although there may be some objection to them, as being either modifiable or sex selected. I agree with Hooton that this list offers a good working basis, and that his definition of a Race is a good one.

De Quatrefages (29b) divided man into three races, White, Black and Yellow, with the Oceanic and American as mixed races; not that color is the most important character that differentiates them, but that it is easily seen and understood. Haddon (39) uses terms of hair form to distinguish the three races; this is a better differential character than the skin color. Hrdlička groups the Oceanic and American peoples with the Yellow race as the Yellow-Browns, and this is justified because of their origin, although a large Negro element is to be found in Oceania, and also in southern Asia.

According to Hooton (39) a race is a

"great division of mankind," therefore he may exclude all but the three great races of man. Other peoples such as the Australians, Ainos, and Eskimos are remnants or fragments of man who have been isolated under peculiar conditions and have inbred more or less until they have in small numbers become quite homogeneous. Groups of a similar kind exist in a more or less isolated condition and may be segregated as Sergi (61) segregated the Mediterranean Race, or Peake (57) the Prospector type, or Ranke the Big-cerebellum-box-headed-Bavarian, or as the type of Beddoe, of Deniker (29), of Ripley (59), of Dixon (30), and of a great many others have been segregated.

Sergi (61) distinguishes many types of skulls as Mediterranean by an elaborate classification and with laborious perseverance, and some verity. He was the first to establish the Mediterranean Race (?) as a distinct entity, yet there are many characters besides those of the skull that have been utilized to differentiate this race.

Peake (57) describes the Prospector type in such a way as to resemble a specialized Alpine stock similar to the Adriatic of Deniker,—tall, heavy, broad, dark, a leader in business and probably wealthy.

The Big-cerebellum-box-headed-Bavarian of Ranke as described by Beddoe speaks for itself.

Deniker (29) divided Europeans into six types or as he called them, races, and four sub-races: 1) Nordic and Sub-Nordic; 2) Eastern, the same as the Celt above, and Sub-Eastern or Vistulian; 3) Ibero-Insular or Mediterranean, or *Homo meridionalis;* 4) Western, Cevenole or Alpine, also called Celtic, Celto-Slav, Rhetian, Ligurian, or Celto-Ligurian; 5) Littoral, Atlanto-Mediterranean, or Cro-Magnon, and Sub-Littoral or Northwestern; 6) and Adriatic or Dinaric, and Sub-Adriatic similar to the Sub-Nordic although semi-Alpine. The Littoral is an enlarged Mediterranean or a modified Cro-Magnon, and the Sub-Littoral is a mixture of Nordic and Mediterranean. The Adriatic is an enlarged Alpine type, and the Sub-Adriatic is a mixture of the Alpine and Nordic. This is one of the best classifications of the types of Europe, but it takes in several local varieties. More types could be added, or the types could be grouped into fewer varieties.

The work of Ripley (59) is exhaustive and very good because it confined itself to the few fundamental types that may be distinguished, and located them in a general way. The Alpine, Nordic and Mediterranean represent at least recognizable types, but Ripley shows too much or too little. Too much stress is laid on cephalic index, stature and pigmentation. Too little stress is laid on non-adaptive characters. All the people of Europe are not Alpine, Nordic or Mediterranean. Many varieties are to be found. Nor will all the varieties together include all the people.

Other methods than those used by Ripley and Deniker must be utilized to get at the true conditions. On the strength of this, when I first examined the students at the University of Michigan, and later the students in Manila, at the University of the Philippines, I grouped them as if they were polyhybrids resulting from a cross of two different stocks. I obtained eight forms that showed almost the same percentage proportions as those obtained by Price and Drinkard upon the crossing of the Yellow Pear with the Honor Bright Tomato, and almost the theoretical requirements for a Mendelian trihybrid.

This method was discarded because it was inadequate to explain all types, and because too few characters could be used.

Dixon (30) has recently applied the same method to a study of the distribution of human types from a few factors of skull form. There is a great deal of truth in his results, some of his types are entities, but not enough characters were used; his material was inadequate; and he did not select non-adaptive characters. After we have learned more about the intricate details of Mendelian inheritance we may hope by the use of proper methods, proper characters and studies through three or more generations of living men to attain satisfactory results.

Günther (38) has recently classified the races of Germany as Northern or Nordic, Western or Mediterranean, Eastern or Alpine, and Dinaric. The physiognomy of the Dinaric is striking and more or less uniform in his numerous illustrations, but the type seems to be similar to the Littoral of Deniker, and Deniker calls his Littoral type Dinaric. The head is short and high like the Armenoid head and some artificial deformation is suggested by its appearance.

The evolution of man from the Neanderthal form that existed in Europe about 30,000 years ago is being more surely traced as new discoveries are made. Scattered forms throughout Europe, such as the Spy skeletons (47), the Chancelede skeleton (56), Aurignacian forms (47), the Krapina finds (36), and more recently the discoveries in Bohemia (52) and Moravia (63) which have not yet been fully worked over and completely described, give assurance that these forms continued to our day in modified condition, changing through the Brno, Brüx, Combe-Capelle, Cro-Magnon and later types into the modern types of Europe (70).

Hrdlička has repeatedly called attention to this in his public and private lectures. Man has evolved in masses and in isolated groups, with modifications of one kind or another, into multiple forms in Europe. In some places the primitive forms have been retained more or less modified as in some of the islands of Denmark (64) where Neanderthaloid forms have been measured in anthropometric surveys. In other places the forms have become extremely different from the original, as in the transformations from the Combe-Capelle type to the small, slender stock, as traced and described by Fleure (32) in Wales and Ireland. Some of the Combe-Capelle stock has remained less modified than others, producing what has been called the Old Black Breed of Scotland, Ireland and Wales.

There has been a gradual change in the different continental and coast areas that makes the interior peoples of Europe different from the coast peoples. The heavy, stocky kind of the interior is different from the small slender kind of the coast. Thus we have the Mesomorph and the Hypermorph respectively.

Montelius (55) traces the present stock of Nordics in Sweden to the prehistoric form found there 10,000 years or more before our time, and probably derived from a form similar to the Cro-Magnon in France. There is evidence of the persistence of the Cro-Magnon (29a) in France today in Dordogne where disharmonic types may be seen (59). No doubt this type spread in western Europe becoming modified with changing conditions. The same stock spread into Asia, and the Steppe folk of Peake belong to this stock.

Hrdlička (48) concludes from a study of the peopling of Asia that the earliest people were Negritos from Africa; the next stock was the "Australoid" from a form in Europe like the Aurignacian and late paleolithic; the rest of the popula-

tion came from the west, northwest, and north, spreading in waves with subsequent mixture. This population gradually spread over the whole of Asia and out into the seas, across Japan, and over variable practicable routes to America, some of it from the Pacific Islands, some through Alaska. The Negro and Negrito are from the old Mediterranean and European stock at an earlier period than the movement into Asia, probably early Neanderthal, and as they moved through Africa they developed into the big Negro and the little Negrito. The earliest known cradle of humanity was in Western Europe. My own conclusions have been practically the same from a study of the living, although carried out independently and in a different way.

It would appear that a big and a little stock are apt to develop from the same original, as the Cro-Magnon and the Combe-Capelle, the Nordic and the Mediterranean. Then other forms come from these. The round heads seem to come from the long heads. The long headed Negroes produced the round headed Negritos, the long headed Europeans produced the broad headed. The Nordic produced the Celt, the Littoral produced the Alpine, and the Mediterranean has produced a small, broad headed, short nosed, short faced stock that is frequently confused with the Alpine. The broad heads of Mugem, Furfooz, and other places may be Mediterranean rather than Alpine.

Harold Peake (57) has recently traced the Bronze Sword and Iron Sword people through Europe from about 4000 B.C. almost to our era. About 4000 B.C. Alpine peoples occupied the mountains of central Europe, coming originally from Asia Minor, and Nordic-Steppe folk mounted on horses were driving cattle from pasture to pasture over steppe, and through forest. About 3000 B.C. a drought caused some of the steppe folk to emigrate and they reached the Baltic, Belgium, Switzerland and Hungary. This was followed by other emigrations. The first emigrants had leaf-shaped bronze swords, and as they conquered they mixed with the Alpines producing a Celtic stock that was partly blond. They conquered nearly all of Europe except the Iberian peninsula. Later the Iron Sword people of the same Nordic-Steppe stock conquered almost all of Europe, but not Scandinavia or Britain. The Nordic-Steppe people were like the Kurgan builders of Russia, the people of the Row Graves in Germany, not unlike the Scandinavian Nordic type and the Vikings, similar to a modified form of the Cro-Magnon, and may have had some part in forming the Littoral, Adriatic, and Dinaric types. A stock similar to this has been found among the Himalayas, as in the Sikhs, and among the American Indians. Stocks like the Turks as they were originally, and some of the eastern African peoples were much like these steppe folk. They may be called the Conquering Race because they moved from place to place conquering as they went. Measurements of two persons derived from that stock as found at present in America are given in table 11.

The Conquering Race is of the Hypermorph type and may be blond or brunette. They are not the extreme Hypermorph which is small and slender and also blonde or brunette. More of the extreme Hypermorphs in America are brunette than blond and more of the Hypermorphs are blond than brunette.

The characters of the Conquering Race are like those of the Caspian Race of Dixon (30) and there is evidence of a distribution of the living similar to that found by him in studying the skeletal

remains. The stock was tall, large boned, long limbed, long headed, large faced, and big nosed. They became more slender, and their physiognomy changed in Europe. They spread over Europe in the late paleolithic period, and from the steppes of Asia they came back into Europe. They went north through Siberia to America, and south to the Himalayas and the Pacific, some going into eastern Africa. Their primary characters have been retained more or less in America, the Himalayas, eastern Africa, and remote places, but in Europe they have become altered. Their color is black in Africa, grayish yellow in Asia and America, and blond or brunette in Europe. This type is closely related to the small, slender Mediterranean type and together they form the most distinct part of the Hypermorph type in Europe, as the Alpine forms the most distinct part of the Mesomorph type.

TABLE 11

Actual measurements of a man and woman of the Conquering Race now living in America

	MALE	FEMALE
Character:		
Stature	183.0	171.3
Sitting height	95.0	89.6
Leg length	88.0	81.7
Arm length	87.0	78.9
Acromion height	154.0	145.7
Head length	20.0	19.9
Head breadth	15.1	15.0
Head height	14.4	14.8
Hand length	19.6	19.0
Hand breadth	9.3	8.3
Nose length	6.2	5.5
Nose breadth	3.1	3.7
Ear length	5.8	5.8
Indices:		
Sitting height / Stature	52.0	52.3
Sitting height / Leg length	110.0	110.0
Sitting height / Arm length	119.2	113.0
Head breadth / Head length	75.5	75.3
Hand breadth / Hand length	47.8	43.6
Nose breadth / Nose length	50.0	67.3
Ear breadth / Ear length	62.0	60.0

Having discussed at some length the conditions of race we may now present a few of the conditions of type or anatomic form. Stratz (65) divided man into three groups, *Protomorphs* or nature folk, *Archimorphs* or highly differentiated peoples, and *Metamorphs* or mixed stocks. The Protomorphs comprise the Australian, Papuan, Hottentot, American Indian, Eskimo, Philippine Negrito, and the Negrillo. As some of these are mixed the classification is not consistent. The Archimorphs are the white, the black and the yellow. We come back to the same classification as that of the races.

Manouvrier (54) was the first to show that two European types exist. He called these the Brachyskéle and Macroskéle with the Mesatiskéle in between. The Brachyskéle is broad in every horizontal measurement, and short in every vertical measurement, but especially in the extremities; and the Macroskéle is narrow in every horizontal measurement and long in every vertical one.

Godin (34) extended the work of Manouvrier on the adult in his own investigations on children, and showed that the differences increase with age. The chief difference is in the leg length in relation to sitting height, or sitting height index. The Brachyskéle has relatively short legs and the Macroskéle relatively long ones. The Brachyskéle and Macroskéle, as selected, represent only the two extremes of the population.

By such a selection greater differences might be shown than by taking each person as was done in tables 6 and 7 for the Mesomorph and Hypermorph. The latter represent the same types as the other two above.

Goldthwait (35) in the Shattuck Lecture for 1915 discussed the types of the White race, dividing them into Broad-back and Narrow-back. He found that the Broad-back was inclined to certain diseases more than the Narrow-back, and the latter to certain other diseases more than the Broad-back. The Broad-back and the Narrow-back are the same as the Mesomorph and Hypermorph and the Brachyskéle and Macroskéle respectively.

Treves (67) studied 200 species of animals in relation to the evolution of the intestinal canal, and concluded that the evolution of different species depends largely upon food environment. He divided them into carnivore, with short intestine, and herbivore, with long intestine. The same condition applies to man where the long lean kind has a short intestine and the broad stocky kind has a long intestine.

Bryant (21) (22) took up this work and from a study of autopsies and the dietary relations suggested more than 100 differences between the two types, —anatomical, physiological, chemical and pathological. There can be no doubt of the value of such work in relation to diagnosis, treatment and prognosis of disease.

Stockard (66) suggests the names Lateral and Linear for two types that are the same as the Mesomorph and Hypermorph, and suggests that the former is low thyroid and the latter high thyroid. The distribution of the types seems to make the suggestion plausible because the Mesomorph is found in continental interiors and the Hypermorph along the coast. Lack of iodine in the interior and presence of iodine in sea water and sea food may account for the differences between the types, at least for the most striking differences. One cannot exclude other factors such as food, climate and habits. The short intestine of the Hypermorph may be the result of concentrated food, and the long intestine of the Mesomorph the result of coarse food of great bulk. The infantile condition of the Hypomorph may be the result of the adverse environment of arctic and tropic regions.

Draper (31) has studied man in relation to disease by reversing the usual anthropometric method of approach. He measured the individuals who had certain definite diseases such as tuberculosis, gastric ulcer, gall bladder infection and pernicious anemia. The result was to find a gall bladder type, a gastric ulcer type, and so on. The gall bladder people in general represent the "sthenic, lateral, or breitwuchs" type and the ulcer cases the "asthenic, linear, or hochwuchs" type. "The ulcer people can never raise their ponderal index above a certain low figure." The ponderal condition of overweight in the gall bladder cases undoubtedly represents a constitutional factor. "The noses of gall bladder people are large in both length and breadth," whereas "the asthma and tuberculosis people have long thin noses." "The ulcer and tuberculosis people have very flat chests, while the gall bladder and pernicious anemia people have deep ones." "The lateral thoracic diameter of the gall bladder people is the greatest. The male pernicous anemia people show the next largest. The tuberculosis and ulcer people have the narrowest chests among the females, and the nephritis hypertension group have the smallest

lateral thoracic diameter among the males. There is a sexual difference in other ways that will be noted later. The tuberculosis and ulcer group in general have flat and narrow chests and the pernicious anemia and gall bladder people have wide and deep chests. The gall bladder and pernicious anemia people have short broad hands, but the tuberculosis, nephritis, and ulcer folk have long narrow hands. The pelvis is broadest in the gall bladder and pernicious anemia people, and the asthma and tuberculosis people have narrow pelves. The above is taken practically verbatim from Draper. It may be seen that the people who have tuberculosis and ulcer have characteristics of the Hypermorph whereas those with pernicious anemia and gall bladder troubles are decidedly of the Mesomorph type. In previous studies (11), (12), (13) of several thousand cases the author showed that tuberculosis and ulcer occur almost entirely in the Hypermorph type, and gall bladder troubles more frequently in the Mesomorph. Not enough cases of pernicious anemia were studied to decide to what type they belong.

Draper brought out some interesting sexual relations in disease and type. "The male and female of the nephritis hypertension people approach one another in their absolute measurements," but "there are only two measurements in the whole series in all the diseases that show practically no sex difference," "The tuberculosis and ulcer people show great differences in point of size in their absolute measurements. But the two sexes are built in practically identical proportions." In some cases the sex characters seem to be suppressed, in others they are paramount.

The physiological aspects of human types are bound up in diathesis, constitution, habitus, temperament and the like. The corset makers of a previous generation had considerable knowledge of human types. There was a small slender and a tall slender form, a small stocky and a tall stocky form, a form like a pyramid and another like an inverted pyramid, a form like an inverted pyramid with the base of a normal pyramid opposed to it, or big in the middle and small at each end, and finally the opposite of the last, a form large at both ends and small in the middle. The first two of these types are Hypermorph and the next two Mesomorph. The other four types are not so common and represent mosaics.

Among the first to call attention to four physiological types are Chaillou (24) and his coworker Mac-Auliffe (25), although they give the credit to Sigaud (62) who originated the terms respiratory, digestive, muscular, and cerebral types. They also call attention to the work of Tricolet (68) on four similar types. These types have become well recognized and are utilized in medical clinics, therefore a few words about each may not be out of place.

Muscular type. The face is rectangular, vertical in front, no prognathism, and the distance from the top of the forehead to the glabella, from the glabella to the nasal spine, and from the latter to the chin are equal. These three parts of the face differ in the other types. The upper part is large in the cerebral type, the middle part in the respiratory, and the lower part in the digestive. The nose in the muscular type is straight or sinuous, high and somewhat rectangular. The neck is broad, well filled with muscle, but not necessarily short. The shoulders are horizontal as are the clavicles and acromion processes. The iliac crests are not very wide, but the costal angle is

about 80°. The profile of the trunk is convex in front and straight behind. The extremities are usually long, and the muscles are strongly developed. There are several sub-types of the Muscular, a Long and a Short, a Musculo-cerebral, a Musculo-respiratory, and a Musculo-digestive. The type makes up about 40 per cent of the population.

The *Cerebral type* appears in about 14 per cent of the people, and is the rarest of all the types, and represents the product of civilization. It occurs more often in late Egypt than in early Egypt (46). It is increasing in those places where civilization is advancing. The type is characterized by a small and slender body, a large and rounded head, remarkably developed upper face and reduced lower face. The frontal and parietal bosses of the cranium are well developed, the side view is spheroidal with a high auriculo-bregmatic diameter. The index is hyperbrachycephalic. The trunk is slender, the extremities short, the hands and feet small. There are mixed types as for the muscular.

The *Respiratory type* occurs in about 30 per cent of people. The middle part of the face is extremely well developed, the nose long, the maxillary bone large, the malar bones prominent, all the accessory sinuses of the nose including the mastoid are large. The eyes are far apart because of the large size of the nasal cavity, and the orbits are well separated. There is superior prognathism because of the large size of the maxillary bones. The face is lozenge-shaped because of its large size in the middle. The cranium is mesocephalic more than in the muscular type. The neck is long and well filled especially about the larynx which is large, with a prominent Adam's apple. The thorax is long and large, and the abdomen reduced by the size of the thorax, which reaches nearly to the iliac crests. All the muscles of respiration are well developed, but those of the extremities are not. The persons are usually thin. The joints are not rough and prominent as in the muscular type nor are they small and graceful as in the digestive type. In the female they are specimens of grace and beauty, tall, delicately molded, with an oval face; they represent the Raphael and Leonardo de Vinci types. The Respiratory-cerebral types are common, but the Respiratory-digestive are rare and the Respiratory-muscular not uncommon.

The *Digestive type* is not common although present in about 20 per cent of the people. The outstanding characteristics are the large lower face, huge jaws and extremely ponderous abdomen. The mandible and zygoma are unusually well developed, and the teeth are large, regular and well formed. As age advances the double or triple chin becomes evident, fat accumulates about the buccinator muscles, the masticators, and the parotid gland about the ear, and this part of the face seems monstrous, and even raises the lobule of the ear and extends it forward. In spite of appearances the trunk is small. Its form is that of a cylinder slightly flattened in front and behind. A pad of fat covers it. The size of the abdomen reduces the size of the thorax considerably, making it short. The extremities are very long, the shoulders broad, the reach much greater than the stature. Mixed types are common, and the Digestive-muscular type is a veritable giant in some cases.

Bauer (5) follows the types of Sigaud and attempts to correlate their predisposition to diseases.

Other types have been added to these. Bach (2) (3) has shown a Wrestling type that appears distinctive after studying 85

measurements, indices and percentage relations of each person. This type is built like an inverted pyramid with a ball, the head, on top of the base. The shoulders are exceptionally broad, as is the thorax. The type is tall and heavy, and the muscles of the chest, arms, shoulders and neck are unusually well developed. The Digestive type, called Pykniker by the Germans, has also wide shoulders but compared with the Wrestler the difference is great. Thirty-three professional wrestlers, 95 amateur wrestlers, 3,457 German gymnasts, 710 students and 33 Pyknikers were compared. Taken in the above order the stature was found to be as follows: 177.3 cm., 169.1, 169.2, 172.5, and 167.9; the weight, 104.5 kg., 68.2, 64.5, 62.6, 73.9; the chest circumference, 117.4 cm., 98.7, 93.7, 88.2, 100.2; the abdominal circumference, 104.8 cm., 79.7, 76.1, ..., 92.4; the shoulder breadth, 42.5 cm., 39.7, 38.9, 38.1, 38.3; the hip breadth, 34.5 cm., 29.4, 28.9, 28.8, 30.5; and the upper arm circumference, 37.2 cm., 30.5, 28.4.

Henckel (41) (42) tries to correlate Habitus, Constitution and Race, but finds considerable difficulty and little correlation. The Alpine and the Pykniker types correspond somewhat, the Nordic and the Leptoprosomic types are somewhat similar, and he includes the Cerebral and Respiratory under the latter but the Sanguine type and the Schizophrenic are minus and plus respectively in head measurements. The Nordic has head length and breadth and cephalic index extremely different from any other type. The curves of the measurements of the Pykniker and Sanguine types are parallel, as are also those of the Muscular and Schizophrenic. The Leptoprosomic are susceptible to tuberculosis and the muscular and digestive are susceptible to aortitis and kidney disease. The Leptoprosomic including the Cerebral and Respiratory types are Hypermorphs, and the Muscular and Digestive are Mesomorph. The Pykniker and Manic-depressive types are related. Asthenic types should be called Leptoprosomic, or Linear, and they are the reverse of the Apoplectic according to Paulsen.

Viola (69) and Frassetto (33) Castaldi and Vannucci (23) follow the types as called Linear and Lateral by Stockard and Hypermorph and Mesomorph by Bean, to which they add a type between the others called the Normal returning to the same types that Manouvrier and Godin found. Frassetto still further divides the types into Microsplanchnic, Mesosplanchnic and Macrosplanchnic, under which he includes Microcephalic, Mesocephalic and Macrocephalic; and he still further subdivides these into Micromelic, Mesomelic and Macromelic, making 27 varieties in each of the three forms. Surely this does not exhaust the possibilities of type forms. They are much more numerous and their name is legion!

Mills (54b) has divided man into six types by the topography of the thorax and abdomen, hypersthenic (very stocky), hypersthenic-sthenic, sthenic, sthenic-hyposthenic, and hyposthenic (very long slender trunks). These may very readily be grouped into three by taking the two extremes, with all the others as intermediate.

Bardeen (4) has produced several masterly monographs on body build in relation to development, in which he concludes that judgment of build from height-weight index is greatly helped if we have some means of estimating relative length of lower extremities and relative adiposity. "Relative length of limbs may be most simply estimated from sitting-height as compared with stature. Relative adi-

posity may be most simply estimated from the relative circumference of the abdomen, or better from its relative antero-posterior diameter, since adiposity makes itself most clearly manifest here." He also concludes that the height-weight index is influenced by post-natal morphogenesis, sex, inherited individual or racial peculiarities, and peculiarities of structure due to habits of living or environment. Later he develops curves and formulae for working out the relative sitting height for comparison in different race, sex and age or other groups which may be of service in future race and type studies.

Davenport (28) from exhaustive studies of the inheritance of body build draws many interesting conclusions. The index of build is best expressed by the ratio of chest diameter to stature, or as that is rarely known, by chest circumference to stature. When only weight is known the best index is weight: $(\text{stature})^2$. The index is 2.52 for males and 2.43 for females. There are marked racial variations in build; there are also geographical differences; but the ontogenetic differences exceed these. The heavy build of the infant corresponds to that of the short-legged anthropoids, and the long-legged, slender build of the boy of 12 years persists in the Nilotic negroes and many low-grade feeble-minded. Changes in build vary with families. The polygon of mass numbers is skew in the direction of slenderness. Diseases of the slender build are tuberculosis, pneumonia, "nervousness," melancholia; of the fleshy build, diabetes, nephritis, dropsy, apoplexy, arterio-sclerosis, and paralysis following. Genetic build is controlled by multiple factors. Slender parents have slender children only, fleshy parents have both kinds. Hereditary factors probably work through the endocrine system. The number of factors involved in fleshy build varies from 1 to 4 or more. The factors influence the functioning of the thyroid, pituitary and perhaps other glands.

Czekanowski (27) uses a four dimensional chart by which four characters may be shown graphically, and with this proceeds to clear up some of the types of Baden and Sweden. The Mediterranean type of Baden is not the small Ibero-insular, but the tall Atlanto-Mediterranean. Red hair is a variant of blond. The Alpine type in Sweden is taller than any other there except the Nordic. The Alpine type is associated with gray eyes and brown hair in Baden and in Sweden.

Pearl (58) has produced several books on human biology of great interest and importance, but his work is not directly related to human types. It would be well to know if the incidence of death from organic heart disease and the influenza death rate both occurred in the Mesomorph. Also it would be of interest to know why influenza and tuberculosis are not so intimately associated as the other two diseases, particularly as tuberculosis is prone to strike the Hypermorph. The death rates of Sao Paulo on the one hand,—mesodermal 3.8 and endo-epithelial 6.2,—and the United States, England and Wales on the other,—mesodermal 4.5 and endo-epithelial 10.0,—may be the result of a larger proportion of the Hypermorph in the Sao Paulo people who come largely from the Mediterranean stock.

Naccarati and Garrett have developed a "morphologic index" by dividing the length of one leg plus the length of one arm by the volume of the trunk. This gives skeletal extremity length and soft tissue volume as factors incompletely. They derive various conclusions as to temperament, intelligence, and physique from their results.

The whole question of physiologic

types hinges upon anatomic form, and this is inextricably bound up with race. With so many workers in the field there is hope of unravelling the threads.

V. SUMMARY

The evidence from human fossils in Europe points to the continuance of man there from the Mousterian period to the present day. Evidence from skeletal remains and from a study of living man indicates that the Black Race developed from the late Neanderthal forms that moved over from Europe into Africa and changed into the big Negro and the little Negrito; and that early "Australoid" forms moved eastward from Europe into southern Asia and the Pacific, followed by later forms of the Paleolithic and Neolithic periods, who came into Asia from the north and west. These continued from time to time over into America to produce the American Indian. Thus the Yellow-Brown race was formed.

There have been changes as the result of selection differing with locality. The interior continental peoples have remained somewhat like the original forms and are Mesomorph in type. The coast peoples have become smaller and slenderer and represent the Hypermorph. Under adverse living conditions the Hypomorph has evolved with a retention of the infantile condition.

It would seem that in Europe the Alpine is somewhat of a myth, the Nordic also and the Mediterranean. Likewise many variants under other names are more or less myths. A part of the population about the Baltic is tall, blond and long-headed, but many other forms are found about the Baltic and so it is about the Mediterranean and in interior continental Europe.

Many synonyms may be used to express about the same condition or type. Broad-back, transverse, lateral, herbivorous, digestive, pykniker, muscular, apoplectic, plethoric, phlegmatic, lymphatic, Brachyskéle and Mesomorph mean about the same thing and so do narrow-back, linear, leptoprosomic, carnivorous, sanguine, respiratory, cerebral, nervous, phthisic, cachetic, choleric, Macroskéle and Hypermorph. The Mesomorph and Hypermorph mean more ontogenetically, phylogenetically and anatomically.

VI. GENERAL CONCLUSIONS

1. The types of the three great races of man have been classified chiefly by their ear form and nose type, but all other available characters have been utilized, especially the stature, sitting height and leg length.

2. Descriptions and illustrations have been given of the three types, Hypomorph, Mesomorph, and Hypermorph, although it is recognized that the descriptions fit only typical individuals. Other persons are more or less like one type or another. Variability is found in the form of blends, mixtures and mosaics.

3. The types are related in a general way to historic and prehistoric groups of men. The Whites are only of the Hypermorph and Mesomorph types; the Yellow-Browns are of the Hypermorph, Mesomorph and Hypomorph types; whereas the Blacks are only of the Mesomorph and Hypomorph types. The Blacks are in some ways more different from the remainder of mankind than are any other people. The most extreme anatomic forms of man are the Negrillo and the extreme form of Mediterranean Hypermorph.

4. Development seems to be from a more or less Hypomorph stage through the Mesomorph to the Hypermorph, whereas evolution seems to have been

from the massive Mesomorph to the extreme Hypermorph on the one hand and the extreme Hypomorph on the other. Evolution in the future is apt to come out of the three great masses of men, White, Black and Yellow-Brown, leaving aside small extraneous groups or fragments of mankind.

5. From previous studies (9) (11) (12) (13), it was shown that the *Epitheliopath* represents the abnormal Hypermorph and is susceptible to diseases of the structures derived from the embryonic ectoderm and entoderm, such as skin, nervous system and alimentary canal. They are also susceptible to chronic diseases such as tuberculosis of the lungs, cancer, pellagra, leprosy and other diseases of malnutrition. The *Mesodermopath* represents the abnormal Mesomorph and is susceptible to diseases of the tissues derived from embryonic mesoderm, such as heart and kidneys, arteries and veins, joints and muscles. They are also susceptible to such acute diseases as pneumonia and typhoid fever. There is a question as to whether there are functional *epitheliopaths* and *mesodermopaths* or not. There may be changes in the soft tissues during the life of a person so that the diathesis may become, for instance, either plethoric or phthisic. The plethoric may resemble the Mesomorph and the phthisic may resemble the Hypomorph. Further studies should be made to determine whether the Mesomorph may become phthisic or the Hypermorph plethoric.

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THE BIOLOGY OF HOST-PARASITE RELATIONSHIPS AMONG PROTOZOA LIVING IN MAN

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I. INTRODUCTION

PARASITOLOGY is a subject of interest to students of various branches of biology. It is taught in the zoology departments of many colleges and universities and in medical schools, especially in schools of tropical medicine. Investigations in this field are carried on principally by zoologists and medical men. Zoologists who are interested in parasitology usually direct their attention primarily to the parasite, whereas most medical men tend to emphasize the reactions of the host. The zoological parasitologist, for the most part, is concerned with morphology, systematics, and life-history studies, and the medical parasitologist with symptomatology, pathology and therapeutics. Only when these two phases of the subject are brought together and when the aspects of the subject peculiar to public health activities are added is a complete program realized; then parasitology becomes the Biology of Host-Parasite Relationships.

The following discussion of the biology of host-parasite relationships is limited to the parasitic protozoa because that is the group of disease-producing organisms with which the writer is most familiar. Probably every species of animal serves as a host to one or more species of protozoa peculiar to itself and these are so varied in their host-parasite relationships that it becomes necessary to further limit our program to a small group of parasites that live in one species of host—man—referring where it seems advisable to related species in lower animals. The relations of the spirochetes to the bacteria and protozoa are still obscure; consideration of the spirochetes is, therefore, omitted here.

One who studies protozoa soon comes to realize that there is no essential difference between free-living species and parasitic species; both types must maintain themselves in their environment and must provide by reproduction for the maintenance of the race. Species living on or within other animals or plants usually exist among relatively more limited and stable surroundings and are more rigidly adapted to one type of environment than are free-living species. Both parasite and host, however, are variable and must be adjusted to each other, thus offering opportunities for the study of the reciprocal influences of organisms. Furthermore, parasites and hosts may, in many cases, be separated and studied apart from each other; this involves experimental procedure without which progress along the lines suggested in our program becomes impossible.

Those who have not interested themselves particularly in parasitology may not be familiar with some of the terms in common use; to these the following definitions may be of value. It is perhaps desirable first to distinguish between parasitism and predatism. A parasite

is an organism that lives on or in and at the expense of another organism without immediately destroying it. A predaceous animal also lives at the expense of other animals but kills them directly and devours them. There are in nature a continuous series of intermediate stages between parasitism on the one hand and predatism on the other.

The term symbiosis was proposed by deBary in 1879 for the constant, intimate and mutually beneficial association of two organisms. Etymologically, symbiosis means simply "living together" and hence should include parasitism, mutualism, commensalism and all other types of consociation, but the term now implies the permanent association of two specifically distinct organisms so dependent on each other that life apart is impossible. When the association is less intimate but each partner benefits the other the term mutualism is sometimes employed. The terms commensalism and inquilinism are often used for still looser associations. Commensalism is applied to the regular association of two definite species of organisms which "eat together at the same table" but not at each other's expense. Very similar in meaning is inquilinism, which is used to describe the condition where one animal lives with another as a cotenant but usually not at its expense.

The origin of these various types of association is, of course, not definitely known, but can be inferred without much difficulty because of the existence of a large number of intermediate stages. That they have arisen many times is indicated by their wide distribution among the phyla in the animal kingdom. The evolution of parasitism is one of the most interesting of all biological problems and, as has been pointed out by several writers, parasites offer particularly favorable material for the study of the course of evolution, since parasites undoubtedly originated from free-living organisms from which they have become differentiated by a sort of superimposed evolution, and in many cases the free-living ancestors of these parasites still exist.

One very striking effect of the parasitic habit is that generally called degradation. This term implies that the parasite has degenerated, but although some of the parts of the parasite undergo degeneration, others become more highly developed. It seems better therefore to speak of the parasitic condition as a specialization rather than a degradation or regression, especially since most parasites are marvelously adapted to their mode of life.

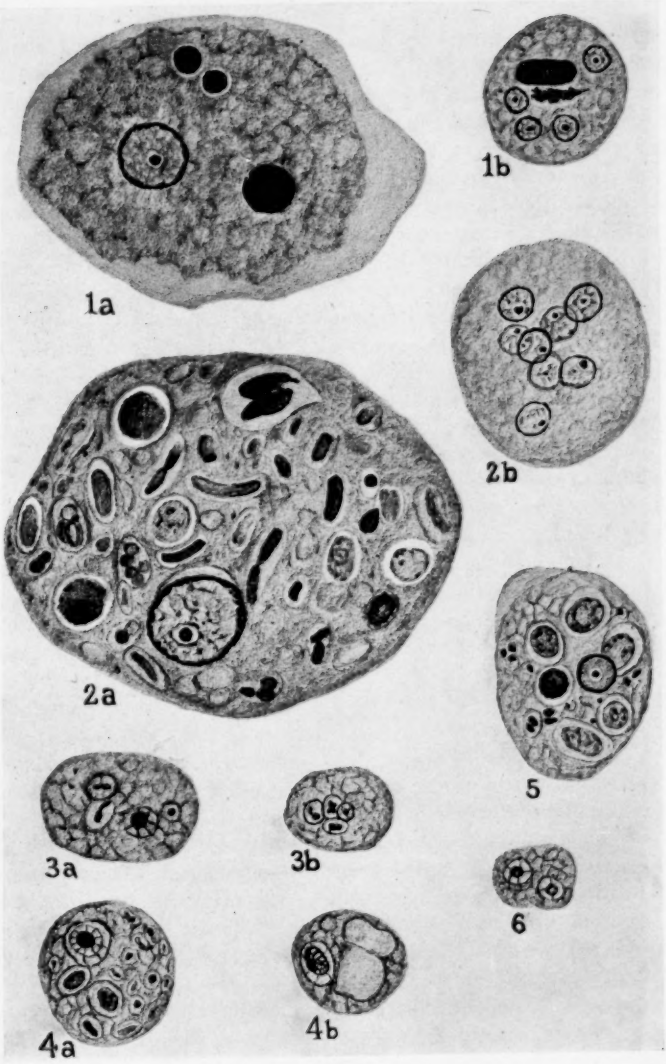
II. PROTOZOA LIVING IN MAN

Each of the four classes of the protozoa includes species that live in man; these are represented by drawings on Plates 1 to 3 and referred to by number below. To the Class Sarcodina belong six species of amoebae, *Endamoeba gingivalis* (fig. 5) in the mouth, and *Endamoeba coli* (figs. 2a, 2b), *Endamoeba histolytica* (figs. 1a, 1b), *Endolimax nana* (figs. 3a, 3b), *Iodamoeba williamsi* (figs. 4a, 4b), and *Dientamoeba fragilis* (fig. 6) in the large intestine.

PLATE 1

AMOEBAE LIVING IN MAN

(All figures magnified about 2000 diameters.)
1a and 1b. *Endamoeba histolytica.* 1a, trophozoite. 1b, cyst. (After Dobell.)
2a and 2b. *Endamoeba coli.* 2a, trophozoite. 2b, cyst. (After Dobell.)
3a and 3b. *Endolimax nana.* 3a, trophozoite. 3b, cyst. (After Taliaferro and Becker.)
4a and 4b. *Iodamoeba williamsi.* 4a, trophozoite. 4b, cyst. (After Taliaferro and Becker.)
5. *Endamoeba gingivalis.* (After Dobell.)
6. *Dientamoeba fragilis.* (After Taliaferro and Becker.)


1a
1b
2a
2b
3a
3b
4a
4b
5
6

The Class Mastigophora contains two groups, six species of hemoflagellates and eight species of intestinal flagellates. The hemoflagellates are *Trypanosoma gambiense* (fig. 18) and *T. rhodesiense* (fig. 19), the organisms of African sleeping sickness; *T. cruzi* (fig. 20), that causes Chagas' disease of South America; *Leishmania donovani* (fig. 21), the organism of kala-azar; *L. tropica* (fig. 22), the etiological agent of oriental sore; and *L. americana* (fig. 23), the causative agent of uta or American leishmaniosis in South America. The so-called intestinal flagellates include *Giardia lamblia* (figs. 13a, 13b), an inhabitant of the duodenum; *Chilomastix mesnili* (figs. 10a, 10b), *Embadomonas intestinalis* (figs. 11a, 11b), *Tricercomonas intestinalis* (figs. 12a, 12b), *Enteromonas hominis* (fig. 14), *Trichomonas hominis* (fig. 9), which live in the large intestine; *Trichomonas buccalis* (fig. 8), an inhabitant of the mouth; and *T. vaginalis* (fig. 7) which occurs in the vagina.

The Class Sporozoa is represented by three species of coccidia, *Isospora hominis* (fig. 15), *Eimeria wenyoni* (fig. 16), and *E. oxyspora* (fig. 17), which penetrate into the intestinal epithelium (there is some doubt regarding the validity of the last two species); three species of malarial parasites, *Plasmodium vivax* (fig. 26a, b, c), the organism of tertian malaria, *P. malariae* (fig. 27a, b, c), of quartan malaria, and *P. falciparum* (fig. 28a, b, c), of estivo-autumnal malaria, all of which invade red blood corpuscles; and one species of muscle parasite of the genus *Sarcocystis* (fig. 25).

Only one species of the Class Infusoria is known with absolute certainty to be a parasite of man; this is the ciliate *Balantidium coli* (fig. 24), which lives in the large intestine and gives rise sometimes to balantidial dysentery. Besides these eight groups, which are recognized by all protozoologists, there is a long list of protozoa that have been described from man about the authenticity of which there is still some doubt.

Each species of protozoon is rather definitely limited to a certain region of the body—organ or tissue. How this localization is brought about can only be conjectured. It may be noted, however, that in most cases the parasites live where their offspring can easily escape from the host or where they are likely to be ingested by intermediate hosts. Most of the species enumerated above live in the digestive tract; this is true of all of the amoebae, coccidia, and intestinal flagellates and of *Balantidium coli;* nine species are blood-inhabiting hemoflagellates and hemosporidia; one species occurs in the vagina and one in muscle. The species of the genus *Sarcocystis* that have been reported rarely in the muscle of man are probably accidental parasites that, through some peculiar circumstances, are rarely able to initiate an infection; but no chance exists of their offspring escaping from the host.

III. EPIDEMIOLOGY OF TRANSMISSION

1. Infective stage

Perhaps the most satisfactory point at which to begin the study of the biology of host-parasite relationships is the infective stage of the parasite. The organisms during the period of the infective stage may be well protected by the host, as in malaria, in which case the infective sporozoites are inoculated directly into the blood of man by a mosquito, but usually are subjected to various environmental factors from the time they escape from the body until they gain entrance into a new host. The idea maintained by many of the older authorities that disease-producing organisms may multi-

ply outside of the host and bring about foci of infection in soil or water has been abandoned since it has been abundantly proved that very little if any increase in numbers occurs under these conditions.

The malarial organism, for example, which was at one time supposed to pass part of its existence in the waters of ponds and streams is now known to lack a free-living existence entirely. The environment of the intermediate host, however, has an influence on the development of the infective sporozoites of the malarial plasmodium since the organism in the mosquito does not continue normal growth and differentiation if the temperature is too low or too high and each species of malarial organism has its own optimum temperature. Similar factors are also involved in the life-cycles of blood-inhabiting protozoa that are insect borne.

Unlike the hematozoa, which are comparatively few in number, most of the disease-producing protozoa of man escape from the body in a cyst-like condition and spend part of their life-cycle outside of the host. The problems encountered during this period are extremely serious and very few of the organisms survive the vicissitudes of a free-living existence. The two principal problems encountered by the parasites are (1) that of withstanding the factors in their new environment and (2) that of developing to the infective stage. The first problem is particularly difficult for protozoa such as the intestinal flagellate, *Trichomonas hominis* (fig. 9), that do not form resistant cysts but pass from one host to another in the active, trophozoite stage. These trophozoites can exist only in a liquid medium and are presumably very susceptible to modifications of temperature, to chemical changes in the environment and to mechanical injury. Most protozoa, however, are protected by one or more resistant walls secreted by the organism, which help prevent loss of water; keep out injurious substances; and guard against molar agents. The terms applied to these resistant bodies are "cyst" (fig. 1b) in the case of intestinal amoebae, flagellates and ciliates, and "oöcyst" (fig. 15) in the coccidia.

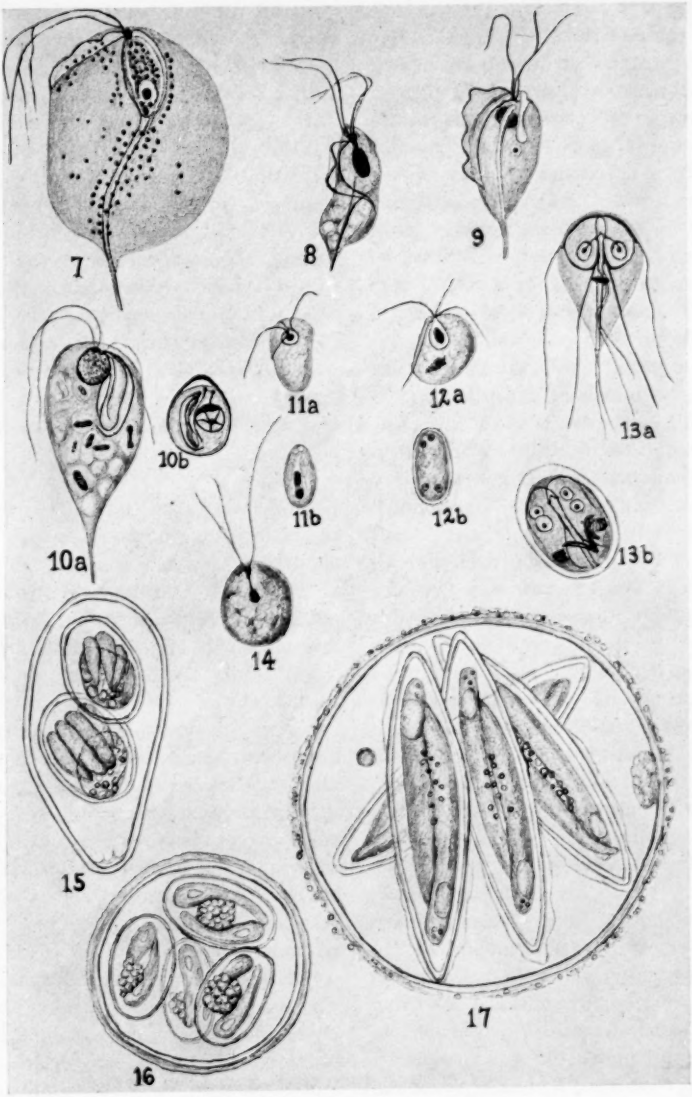
In most cases, probably no development occurs within the cysts after they escape from the body. Thus in the dysentery amoeba, *Endamoeba histolytica*, cysts with from one to four nuclei (fig. 1b) pass out with the feces, but the uninuclear and binuclear immature cysts do not develop further and die more quickly than do the quadrinucleate, mature cysts (Dobell, 1919). The oöcysts of coccidia, on the other hand, continue their development if discharged when still immature. The oöcyst of the most common human

PLATE 2

FLAGELLATES (FIGS. 7 TO 14) AND COCCIDIA (FIGS. 15 TO 17) LIVING IN MAN

(All figures of flagellates magnified about 2000 diameters and of coccidia about 1600 diameters.)

7. *Trichomonas vaginalis*. (After Hegner.)
8. *Trichomonas buccalis*. (After Goodey and Wellings.)
9. *Trichomonas hominis*. (After Faust.)
10a and 10b. *Chilomastix mesnili*. 10a, trophozoite. 10b, cyst. (10a, after Boeck; 10b, after Kofoid and Swezy.)
11a and 11b. *Embadomonas intestinalis*. 11a, trophozoite. 11b, cyst. (After Hegner.)
12a and 12b. *Tricercomonas intestinalis*. 12a, trophozoite. 12b, cyst. (After Wenyon and O'Connor.)
13a and 13b. *Giardia lamblia*. 13a, trophozoite. 13b, cyst. (After Simon.)
14. *Enteromonas hominis*. (After Fonseca.)
15. *Isospora hominis*. (After Dobell.)
16. *Eimeria wenyoni*. (After Wenyon.)
17. *Eimeria oxyspora*. (After Dobell.)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8
9
10a
10b
11a
11b
12a
12b
13a
13b
14
15
16
17

species, *Isospora hominis*, is still in a unicellular condition when it escapes from the body. Its protoplasm then divides into two sporoblasts which become spores by secreting resistant walls about themselves. Four sporozoites are then formed within each spore (fig. 15) (Wenyon, 1915). Presumably not until these sporozoites are fully developed does the oöcyst become infective.

It seems clear from the evidence available (1) that no foci of infection of disease-producing protozoa exist outside of the host and (2) that in the majority of cases certain stages are already infective when they escape from the body and all other stages including trophozoites and immature cysts die outside of the host.

2. *Avenues of infection*

Reaching and invading a new host is perhaps the most serious problem in the entire life-cycle of a parasitic protozoon so far as the maintenance of the species is concerned. Only the smallest fraction of the total number of infective organisms can possibly reach a susceptible animal in which to live, and only the almost inconceivable fecundity of the parasites prevents the various species from dying out. In the most simple cases the infective stage of the parasite is ingested with the food or drink of the proper host. The parasite is passively carried in the medium by which it is surrounded and it is the behavior of the host that leads to invasion. This is the contaminative method of parasite transmission. Laboratory experiments, mostly with lower animals, have established this as an effective method and there is no other obvious way in which infective cysts in nature can obtain entrance to the host.

Cysts remain alive only a few days in undiluted feces, but may live for a considerable period when kept in water. Thus Boeck (1921) found that washed cysts of the intestinal flagellate, *Giardia lamblia* (fig. 13b), lived over two months and those of *Chilomastix mesnili* (fig. 10b) over seven months. These cysts as well as those of certain intestinal amoebae are able to withstand temperatures considerably higher than those normally encountered in nature. The problem of the parasite is to reach the mouth of the host before death results from drying, bacterial action, or starvation within the cyst. A moist warm climate is therefore favorable for transmission. Unsanitary conditions due to neglect on the part of the host are also favorable since this leads to the pollution of drinking water, milk and other food substances. Flies probably play an important rôle in the distribution of the cysts of intestinal protozoa. Root (1921) and others have shown that these cysts may remain alive for a considerable period within the intestine of the fly, e.g., those of *Giardia lamblia* (fig. 13b) at least 24 hours, and may be deposited in a living condition as early as 40 minutes after the fly has fed on contaminated material. In general it may be said that transmission by the contaminative method is more easily effected in rural than in urban communities, and in the tropics than in the temperate regions.

There are three other principal methods of reaching a new host. These are (1) by "contagion" or direct transference from definitive host to definitive host, (2) by inoculation through the agency of an intermediate host, and (3) by "inheritance." The "hereditary" method of transmission does not occur so far as I know in any protozoon living in man; but takes place in a number of parasites of lower animals. For example, the microsporidion, *Nosema bombycis*, that causes *pébrine* in France and *gattina* in Italy, invades the eggs within the ovaries as

well as other tissues of infected silkworms and the spores germinate in the larvae that hatch from these eggs; the young silkworms thus "inherit" the infection. In a similar manner the hemosporidion, *Piroplasma bigemina*, that causes Texas fever in cattle, is transmitted from the intermediate host, usually a tick of the genus *Boophilus*, to its offspring through the egg.

The direct or contagious method of transmission may be brought about in various ways. Among human protozoa the amoeba, *Endamoeba gingivalis* (fig. 5) and the flagellate, *Trichomonas buccalis* (fig. 8), that live in the mouth, no doubt are transferred directly from one host to another by kissing. The flagellate, *Trichomonas vaginalis* (fig. 7), which is apparently widespread among women and has been recorded from the urinary tract of man, is probably distributed during coitus. The high incidence of infection by these flagellates is not generally realized. *Trichomonas vaginalis*, for example, was found by the writer (Hegner, 1925) in vaginal smears from exactly 50 per cent of the women examined at hospitals in Honduras and Costa Rica in the summer of 1924. These organisms might almost be considered ectoparasites since they do not penetrate into the body tissues. Among the lower animals direct contact is responsible for the transmission of certain endoparasites; for example, the hemoflagellate, *Trypanosoma equiperdum*, which lives in the blood of horses in various parts of the world and causes a disease known as dourine is transferred from one host to another through the mucous membranes during coitus.

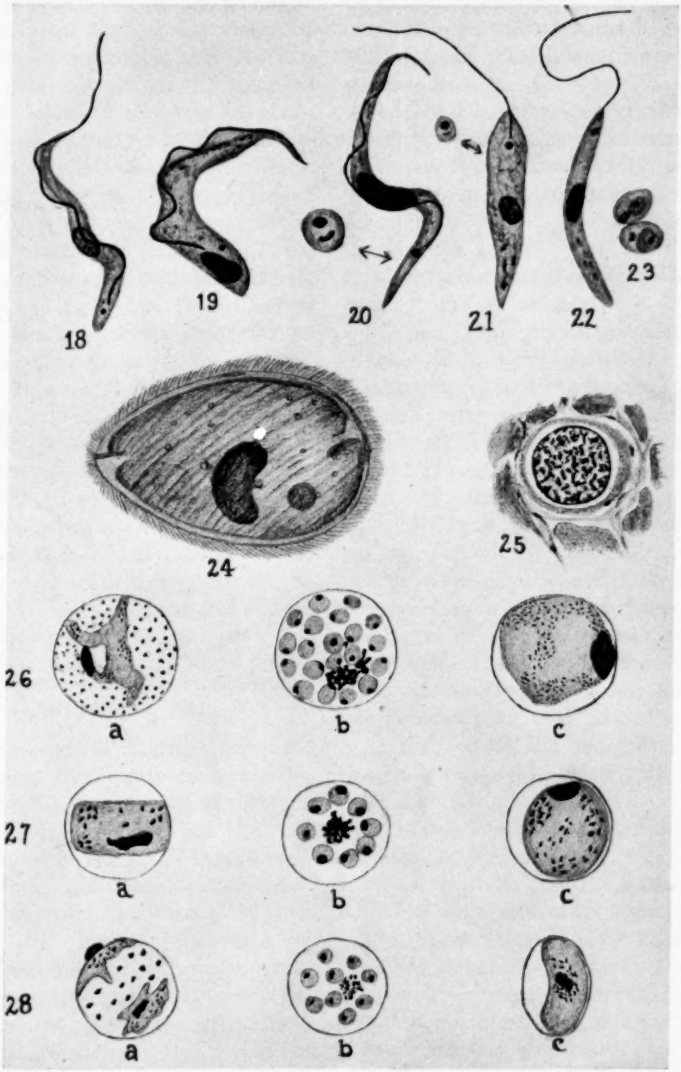
Inoculation by an intermediate host is a very common method of transmission and involves the most complicated behavior on the part of host, intermediate host and parasite. In malaria, for example, only the females of certain species of mosquitoes become infected; these must suck up the blood of malaria patients and do not usually become infected unless this blood contains at least twelve sexual parasites (gametocytes) per cubic millimeter; the external temperature must not go beyond certain limits, as noted above, or the life-cycle within the mosquito is not completed; the mosquito must protect itself from numerous dangers in its environment for from 8 to 18 days depending on the temperature and species of parasite before the infective stage, the sporozoite, is reached; then if a susceptible host chances to be abroad after dusk or at dawn or is unprotected by netting during the night and an infective

PLATE 3

HEMOFLAGELLATES AND SPOROZOA LIVING IN MAN

(All magnified about 2000 diameters except no. 24, about 700, and no. 25 magnification unknown.)

18. *Trypanosoma gambiense*. (After Hegner and Taliaferro.)
19. *Trypanosoma rhodesiense*. (After Hegner and Taliaferro.)
20. *Trypanosoma cruzi;* flagellate stage and leishmania stage. (After Hegner and Taliaferro.)
21. *Leishmania donovani;* flagellate stage and leishmania stage. (After Hegner and Taliaferro.)
22. *Leishmania tropica;* flagellate stage. (After Row.)
23. *Leishmania americana;* leishmania stage. (After Row.)
24. *Balantidium coli*. (After Hegner and Taliaferro.)
25. *Sarcocystis*. (After Baraban and Saint-Remy.)
26 to 28. Malaria parasites within human red blood corpuscles.
26. *Plasmodium vivax* of tertian malaria. *a*, schizont; *b*, merozoite formation; *c*, gametocyte. (After Hegner, Cort and Root.)
27. *Plasmodium malariae* of quartan malaria. *a*, schizont; *b*, merozoite formation; *c*, gametocyte. (After Hegner, Cort and Root.)
28. *Plasmodium falciparum* of aestivo-autumnal malaria. *a*, schizont; *b*, merozoite formation; *c*, gametocyte. (After Hegner, Cort and Root.)


18
19
20
21
22
23
24
25
26
a
b
c
27
a
b
c
28
a
b
c

mosquito chances to encounter him, sporozoites are inoculated during the three or four minutes occupied by the mosquito in getting a meal of blood. The conditions of successful transmission in this case seem so complicated that it is surprising that malaria can continue to exist; nevertheless it is today economically the most important of all diseases in tropical and semitropical countries.

Other human diseases, the protozoan organisms of which are transmitted by inoculation, are African sleeping sickness, due to trypanosome flagellates (figs. 18, 19) and spread by tsetse flies; Chagas' disease of South America, due also to trypanosome flagellates (fig. 20) and carried by bugs of the genus *Triatoma*, and possibly kala-azar (fig. 21) and other leishmanioses, the method of transmission of which is still unknown. Many of the protozoan parasites of lower animals are also transmitted by the inoculative method, the relations of host and parasite in each case being usually as complicated as in human malaria and of almost infinite variety.

IV. HOST-PARASITE RELATIONSHIPS DURING A NATURAL INFECTION

The term natural infection is used here to designate an infection in nature during which the parasite is able to pass through its life-cycle successfully and provide infective stages for the invasion of a new host or intermediate host. In contrast to natural infections, are conditions that result from the invasion of hosts that may be called foreign, refractory, accidental or casual,—terms that are fully explained below under the subheading Host-Parasite Specificity.

1. The course of infection

a. Parasitological periods (see text figure). (a) The *Prepatent Period* extends from the time the infective parasites enter the body of the host until their offspring can be recovered by the usual laboratory methods. The length of this period obviously depends to some extent on the character of the laboratory technique employed.

(b) The *Patent Period* covers the interval during which the parasites can be demonstrated by microscopical technique. The parasite number undergoes a *Rise* during this period, reaches a *Peak* and then suffers a *Fall*. The patent period ends when the parasites can no longer be found in the blood, feces, etc.

(c) In many infections the patent period is followed by a *Subpatent Period* of indefinite length. During this period parasites can not be recovered by the usual laboratory methods but their presence can be proved in various ways depending on the species of parasite. For example, protozoan cysts may disappear from the stools but reappear after a few days, weeks or months have elapsed; and malarial parasites may no longer be demonstrable in the blood of a host but may again become evident during a subsequent relapse. In bird malaria the subpatent period may extend over several years, i.e., from the end of the acute attack until the death of the bird; during all this time parasites cannot be found in the blood by the usual technique, but their presence can be demonstrated by inoculating some of the blood into a fresh bird, in which an acute attack develops.

The subpatent period may be followed by a second patent period during which the parasite number rises, reaches a peak, and falls but often does not rise as high as in the primary attack.

b. Clinical periods (see text figure). (a) The *Incubation Period* extends from the time of the entrance of the parasites until symptoms appear. This period is usually

longer than the prepatent period, but may be shorter. For example, in cats infected with the coccidion, *Isospora felis*, diarrheic symptoms appear before oöcysts are recoverable in the feces. As indicated in the text figure the number of parasites usually increases considerably before symptoms become evident. The curves as given probably do not represent actual conditions in any specific protozoan infection but are meant to indicate that symptoms disappear, but later with the recovery of the host.

(d) In diseases characterized by relapses one or more *Latent Periods* may be present. During these periods the causative organisms are too few in number to bring about symptoms, but after intervals of indefinite length, some change occurs in parasite or host or in both that results in an increase in parasite number and a reappearance of symptoms.

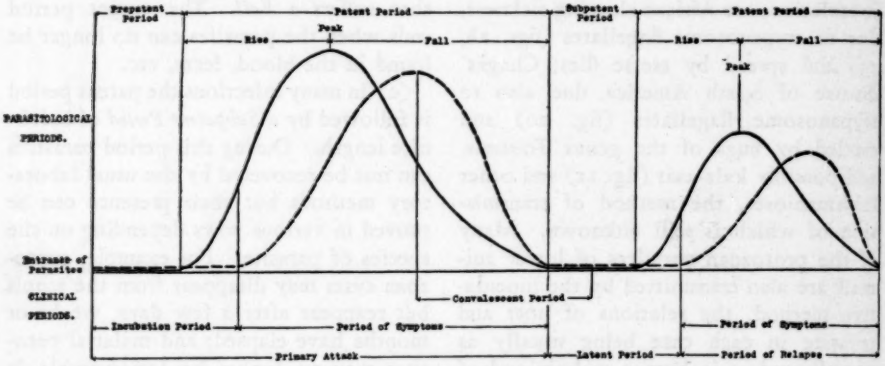


FIG. 1

This illustration is intended to represent by means of curves the parasitological and clinical periods in the course of infections with pathogenic protozoa. It represents in a general diagrammatic way the course of natural infections, consisting of a primary attack followed by apparent recovery of the host. This completes both the parasitological and clinical manifestations of disease in cases such as oriental sore in which one attack gives immunity. In other diseases, however, such as amoebic dysentery and malaria, the primary attack is often followed by a symptomless period when the parasites are latent. Eventually the parasite number again increases, symptoms reappear and the host is said to suffer a relapse. The terms used are fully described in the text.

(I am indebted to the members of my Seminary in Protozoology and especially to Dr. Justin M. Andrews for various suggestions in preparing this diagram.)

in general the increase in parasite number precedes the appearance of symptoms and that increases and decreases in the severity of the symptoms follow the rise and fall in parasite number.

(b) The *Period of Symptoms* begins when the incubation period ends and ends of course with the cessation of symptoms.

(c) The *Convalescent Period* is represented as beginning at the point of maximum symptoms. It ends, not when the

(e) The reappearance of symptoms following a latent period is known as the *Period of Relapse*.

2. *Distribution and localization of parasites within the host*

a. Distribution. As already noted protozoan parasites may gain entrance to their natural hosts by way of the mouth in contaminated food or drink, by direct contact, by inoculation through an inter-

mediate host and by "inheritance." The distribution of the protozoa after they enter the body is at first due almost entirely to the activities of the host and is determined by the point and method of entrance. Blood-inhabiting species, such as malarial organisms and trypanosomes, are rapidly carried to all parts of the body in the blood stream; intestinal-inhabiting species are transported with the food through the esophagus and stomach and into the intestine. Species that are transmitted by contact remain usually in the region of entrance, e.g., in the mouth or genital cavities.

b. Primary site of infection. Different species of protozoan parasites become localized in different organs, tissues or cells of the body depending on various factors. Certain parts of the body are more frequently affected than others, e.g., the blood and intestine, a fact that is probably vitally associated with the necessity of the offspring to escape from the host. The parasites may be (1) coelozoic, i.e., localized in cavities, such as the digestive tract, cœlom or body cavity, blood or lymph spaces, and genito-urinary cavities, or (2) histozoic, i.e., within the tissues, where they may live among the cells (intercellular), within the cells (intracellular or cytozoic), and even within the nuclei (intranuclear). The factors that are responsible for localization are not well known. The parasites are subjected to various conditions in their environment just as free-living protozoa are in theirs; they must protect themselves from injurious agents, such as secretions and excretions; must reach a location where the proper nutriment is available; must possess some means of fixing themselves in a favorable situation; and must be able to carry on reproductive processes.

Certain intestinal flagellates of man are of particular interest for purposes of illustration (Hegner, 1923). The optimum habitat of *Giardia lamblia* (fig. 13a) seems to be the lumen of the duodenum whereas that of *Trichomonas hominis* (fig. 9) is the lumen of the large intestine. The contents of the duodenum are mostly sterile and consist of products of digestion that pass through from the stomach to the jejunum and of various secretions from the stomach, liver, pancreas and intestinal wall. *Giardia* has no mouth and does not ingest solid particles of food and, so far as is known, does not destroy the tissues of the host; its nutriment is absorbed through the surface of the body. Just what part of the material by which it is surrounded is utilized has not been determined. All inhabitants of the small intestine must maintain their positions against the action of peristalsis. *Giardia* is able to do this because of the presence of a sucker-like disc with which it fastens itself to the surface of the epithelial cells. Spaces among the intestinal villi are also of value since they furnish a haven where downward currents are less pronounced. *Trichomonas*, on the other hand, never occurs in the duodenum, unless it is just passing through, and is seldom encountered in the jejunum or ileum; its favorite habitat is the large intestine and especially the cecum. Experiments carried on by the writer with the trichomonads of rats (Hegner, 1925) indicate that these flagellates, as well as the species (*Trichomonas hominis*) that occurs in man, infect new hosts in the active, trophozoite stage and are carried through the mouth, esophagus, stomach and small intestine and into the large intestine unharmed and still able to set up a new infection. Thus when rats were fed milk containing active specimens and killed and examined within from one-half hour to two hours later, it was found in one case that the flagellates

had passed through 780 mm. of intestine and had reached the cecum within one-half an hour. The experiments indicated that the trichomonads are unable to maintain themselves against the action of peristalsis but are carried directly to the large intestine; here they find conditions such that they are able to swim against the slow movement of material toward the outside, especially when they get into the eddy-like contents of the cecum. There is some evidence that movement of the trichomonads is partially inhibited in the stomach and anterior portion of the small intestine, but regained as the large intestine is approached. In the large intestine nutritive conditions are favorable since *Trichomonas* has a mouth and may ingest solid food particles which are present there in abundance.

Localization among tissue parasites offers many problems that are still unsolved. What factors influence the sporozoites of malaria to attack the red blood cells, and those of the coccidia to attack the epithelial cells of the intestine? What causes *Endamoeba histolytica* (fig. 1a) and *Balantidium coli* (fig. 24) to penetrate the intestinal wall, whereas *Endamoeba coli* (fig. 2a) and *Endolimax nana* (fig. 3a), which are also inhabitants of the intestine do not? It may safely be said, that we really know almost nothing about the mechanism of localization of any human protozoon.

c. Secondary sites of infection. Many protozoa become localized in a particular organ or tissue and do not spread to other parts of the body. A few, however, bring about secondary foci of infection in other regions. This requires in the first place either movement on the part of the parasite from one place to another or activities within the host that passively transport the parasite to new situations. The circulatory system of the host is the most important distributing agency. For example, the dysentery amoeba, *Endamoeba histolytica* (fig. 1a), sets up a primary infection in the large intestine; specimens may enter the blood stream in the capillaries of the intestinal wall and are carried to all parts of the body; frequently the liver becomes a secondary site of infection and an amoebic liver abscess results; less often amoebic abscesses occur in the lungs and brain, and amoebae have been discovered in many other parts of the body. Recently Kofoid (1923) has described dysentery amoebae from bone and believes that they are responsible for Ely's second type of arthritis; he believes also that these amoebae may be the etiological factor in Hodgkin's disease and in some cases of chronic neurasthenia and subnormal health; the evidence for this is as yet incomplete. It is obvious that amoebic abscesses may occur in any part of the body provided local conditions are favorable. Just what factors favor the localization and multiplication of the amoebae in liver, lungs and brain and prevent infections in other parts of the body are not clear.

The details of the distribution and localization of parasites within the host are still to be determined, but it may be said in general that distribution is due primarily to the physiological activities of the host, and localization to host-parasite interactions, the parasites setting up an infection wherever favorable conditions exist.

3. Passive (natural) resistance of the host

The number of species of protozoan parasites that are able to bring about infections in man is no doubt very small compared with the number that gain access to his body. The malarial organisms of birds may be inoculated into the

blood of human beings by culex mosquitoes, and the cysts of intestinal protozoa of domesticated animals may be ingested with contaminated food but no infections result. Two principal factors probably account for the success of certain species and the failure of others; these are (1) inability on the part of the parasite to withstand conditions within the host, and (2) failure on the part of the host to provide suitable stimuli for the excystation of encysted forms.

The obstacles that must be met by the parasite at the beginning of an invasion constitute the passive, or natural, resistance of the host. This type of resistance is in part due to the nature of the host without respect to ancestral relations with the parasite or may in part have been built up during the course of evolution as a protection against infection. The changes in the environment of an intestinal flagellate such as *Trichomonas hominis* (fig. 9) which is carried from the outside into the digestive tract of a new host are very striking; light gives way to total darkness; the temperature is constant (98.6°F.); the medium is dense and viscous; chemical conditions become complicated by digestive juices, products of digestion and biochemical products secreted by the host; food conditions are different; and the products of bacterial decomposition are abundant and varied. Somewhat similar changes are encountered when blood-inhabiting species are inoculated into man by mosquitoes (malarial organisms) or tsetse flies (trypanosomes, fig. 18).

A parasite may successfully withstand all these conditions but still fail to bring about an infection because of the absence of factors necessary, for example, to weaken the wall of a protozoan cyst and allow the organism within to escape. The literature of protozoology contains many reports of human "intestinal" protozoa on the basis of specimens found in the feces which were not active within the intestine but had passed through in the cyst stage and had emerged only after the feces were passed; these are "coprozoic" protozoa, a considerable number of which have been described.

4. Passive (natural) resistance of the parasite

If some parasites were not able to overcome the obstacles presented by the host, animals would be totally free from parasites. Thus far no such animal has been discovered. This passive resistance of the parasite, as in the case of that of the host, may have no relation to ancestral infections or may be due in part to evolutionary processes. Whether the resistant coverings of protozoan cysts serve to enable the parasite to reach a certain location within the host or are more important as a protection against injury during their life outside the host it is not possible to decide with certainty. It is known that such cysts will survive when subjected to strong solutions of various chemicals and might therefore easily withstand the body juices of the host. It is also known, as pointed out above in the case of *Trichomonas hominis*, that active trophozoites may pass unharmed through the digestive tract and set up an infection in the cecum. The value of the cyst wall as a means of resisting conditions within the host is therefore very doubtful.

Every animal is able to exist in an environment in which the various factors cover a considerable range, i.e., the optimum conditions are not necessary, although they may be desirable, for the maintenance of either the individual or the race. Protozoan parasites that are natural to a particular host are accordingly able to withstand considerable changes

in temperature; are not affected by the change from light to darkness or *vice versa;* and do not succumb to complex chemical changes nor to increases in the density of the surrounding medium when taken into that host; but why these same parasites are not able to live in nearly related hosts is a problem of great difficulty. Why, for example, is the organism of human malaria able to live in man and not in other species of mammals? Why are the sexual stages of the malarial organism of man stimulated to continued development in the stomach of certain species of anopheline mosquitoes and not in others? Why are the giardias of man unable to live in the duodenum of rats, and those of rats in the duodenum of man? These questions can only be answered when we know more about the passive resistance of the host to the parasite and that of the parasite to the host.

5. The parasite's method of attack

The character of the attack of the parasite on the host is of vital importance not only to the host but also to the parasite. It is obvious that the degree of pathogenicity depends on which organs or tissues are invaded, and on the degree and rapidity of tissue destruction or toxin production, since slight injuries inflicted slowly are usually repaired by the host; whereas serious injuries that are quickly produced lead to symptoms. The association that exists in most cases of parasitism is such that the parasite is able to live and reproduce for many years within the host without apparent injury to it. If the host develops severe symptoms both it and the parasites are in danger and if the host dies the parasites die with it. This type of parasitic attack is unusual and is considered to represent a comparatively recent association, since most parasites live in harmony with their hosts—a condition that is supposed to have developed during the course of evolution.

Types of parasitism are distinguished largely on the basis of the method of attack of the parasite. Among the amoebae living in man, for example, is *Endamoeba coli* (fig. 2a) which inhabits the lumen of the large intestine where it probably lives on food taken in by the host; this type of parasite is known as a commensal and is sometimes termed a food-robber. It does not live in any other species of host nor outside of the body and is therefore a permanent, obligatory parasite and non-pathogenic. Another species of the same genus, *Endamoeba histolytica* (fig. 1a), also lives in the large intestine of man but feeds on tissue elements which it apparently dissolves with the aid of proteolytic enzymes that it secretes, or engulfs *en masse*. Usually the host is able to repair the tissue as rapidly as it is injured, but often the parasites gain the upper hand and amoebic dysentery results, sometimes ending fatally. This organism is a permanent, obligatory parasite that is always pathogenic and sometimes lethal. Other parasites penetrate tissue cells and develop within them at the expense of the surrounding protoplasm. To this type belong the coccidia that live on cells of the intestinal epithelium and the malarial organisms that destroy red blood cells.

During the destruction of tissues by the malarial parasite there are liberated into the blood debris from the broken-down cells and waste products excreted by the parasite or resulting from digestion within the cell. Besides this, parasitic protozoa may produce toxic substances or zoötoxins. Almost nothing is known about these but that they exist is certain and that they act much like bacterial toxins is probable.

6. Changes in the host caused by the parasite

The reactions of hosts to infection may be considered under the headings symptomatology, pathogenesis and immunology. If the parasite lives on the tissues of the body or injures the body in any way it is pathogenic. If the injuries are severe, changes occur in the functions of certain organs sufficient to bring about symptoms. In certain cases the body reacts to the infection by building up a resistance to the parasite which we call immunity.

a. Symptomatology. The symptoms that are characteristic of the various diseases due to parasitic protozoa are in most cases well known. Comparatively little is known, however, regarding the genesis of these symptoms. The Century Dictionary defines a symptom as "one of the departures from normal function or form which a disease presents, especially one of the more evident of such departures." In other words, symptoms arise when the function of an organ is modified. Usually one species of parasitic protozoan brings about a large number of symptoms since more than one organ may be disturbed. Some of these are localized at the point where injury is being done, whereas others appear at a distance.

The most recent and probably the most successful attempt to determine the mechanism of symptom production is that of Sir James MacKenzie (1923). His argument is as follows: Symptoms are produced by organs whose functions are stimulated to unusual activity, or depressed or suspended. Functional activity is dependent on the cells of the organ and on the nerves and other agents that regulate the activity of these cells. There is formed a reflex arc consisting of a receptor which receives the stimulus, an afferent nerve which carries it to a nerve center, and an efferent nerve which conveys it to the effector. A modification of any part of this arc results in an abnormal response, i.e., a symptom. The effector may be a muscle, gland, or the sensorium.

The genesis of symptoms is open to experimental study, such as that of Brown (1912) on malarial pigment (hematin) as a factor in the production of the malarial paroxysm. Brown obtained hematin from the blood of a rabbit, ox, and dog and used rabbits as experimental animals. Single or divided doses in alkaline solution of from 1.3 to 28 mgm. per kilo of body weight were injected intravenously, corresponding to the quantity liberated in cases of human malaria when from 0.3 to 7.5 per cent of the red blood cells are infected. Every dose gave positive results that must have been due to the hematin. There was a definite temperature response in proportion to the dose with a sharp rise to fastigium in about one and one-fourth hours, then a slight fall for from 30 minutes to one hour, followed sometimes by a second rise, and finally a very gradual descent to normal in several hours. Soon after injection the rabbits exhibited convulsive tremors or shivering and the ears became cold—as much as 30°F. below the rectal temperature; this period of chill lasted from 45 minutes to one hour. The paroxysms observed were practically identical with those of human malaria and the conclusion was reached that the toxic action of the hematin is, at least in part, directly responsible for these symptoms.

b. Pathogenesis. Many of the protozoa of man are not pathogenic so far as is known; this is true of *Endamoeba coli* and other commensals. A few, such as *Endamoeba histolytica*, the coccidia and malarial organisms, are unable to exist without direct attacks on the host tissues. These

attacks bring forth more or less definite responses on the part of the host and usually a rather definite series of changes occur during the course of the infection. This series never proceeds beyond the earlier stages in contact carriers (see below) and stops short of the end when the patient is treated or undergoes spontaneous recovery. Only when the death of the host ensues may the final stages be observed. Each parasite maintains its own method of attack and the host responds usually in a perfectly definite way to the inroads of each species of parasite. The changes in the host have definite effects upon the progress of the parasitic attack and it is thus possible to obtain a dynamic view of host-parasite reactions during the course of the infection. The complete pathogenesis has not been worked out for any human protozoon. Experimental studies are possible with lower animals, e.g., amoebiasis in cats, malaria in canaries, trypanosomiasis in rats, etc., and most of what we know of the pathogenesis of protozoan diseases has been gained in this way, but the complete story for any one of them is not yet possible because of lack of observations.

The pathogenesis of intestinal amoebiasis is perhaps as easily studied as that due to any human protozoon. The amoebae are supposed to emerge from the ingested cysts in the small or large intestine. They creep about on the intestinal epithelium and erode the cells by means of a ferment which they apparently secrete. As a result of this the surrounding capillaries become dilated. Continued erosion leads to the formation of ulcers and if the injured tissues are not regenerated rapidly the irritation of the intestinal wall brings on the exudation into the lumen of the intestine of large quantities of serous fluid and peristalsis is greatly increased. The result is diarrhea. The formation of purulent and bloody discharges, which are characteristic of dysentery, may follow.

c. Immunology. The subject of immunity to protozoan infections is in its infancy and the little we know about it at present is based on epidemiological observations and on animal experiments. That hosts differ considerably with respect to natural resistance to various protozoan diseases is evident since many individuals do not become infected although they are undoubtedly invaded by the parasites. Acquired resistance has been demonstrated in certain cases. For example, one attack of oriental sore due to *Leishmania tropica* (fig. 22) confers immunity to further infection, and experiments indicate that partial immunity is induced to this organism in dogs and monkeys. On the other hand kala-azar, which is caused by a closely related organism, *Leishmania donovani* (fig. 21), does not produce immunity against reinfection. A tolerance to malaria has been observed and an immunity to this disease may even be acquired. Thus children in an endemic region become infected when infants and, if they recover, may be reinfected year after year until by the time they are ten years old they cease to show symptoms although they possess enlarged spleens and have parasites in their blood. When these children become adults they are immune as evidenced by a decrease in the size of the spleen and by the absence of parasites from the blood.

Very little is known about the resistance of man to trypanosome infections but a number of important investigations have been carried on with animals. The most important recent researches are those of Taliaferro (1926) with *Trypanosoma lewisi* in rats. If no resistance were encountered when trypanosomes are inoculated into an experimental animal the

organisms would increase according to a geometrical progression series and the death of the host finally ensue. This is what appears actually to occur when *Trypanosoma brucei* is inoculated into a rat. If the parasites do not increase in this way then some type of resistance is in operation. In infections of rats with *T. lewisi* three types of resistance become manifest "(1) the retardation and final inhibition of reproduction by about the tenth day, (2) the sudden destruction of the majority of the parasites between the eighth and twelfth days, and (3) the eventual total destruction of the parasites which terminates the infection and may take place from a few days to several months after the first crisis." Taliaferro has demonstrated the formation of a reaction product in the blood serum which totally inhibits the reproduction of the trypanosomes by about the tenth day. Serum from such an animal when injected into a fresh rat will prevent the reproduction of trypanosomes in it thus furnishing an excellent example of the passive transfer of the immunity from an infected to an uninfected animal. There is no definite evidence as to what causes the destruction of most of the trypanosomes between the eighth and twelfth days but the blood serum evidently acquires rather suddenly a trypanolytic property. The final destruction of trypanosomes which terminates the infection seems to be due to a lysin. The immunology of protozoan infections presents a large and fascinating field for investigation.

7. *Changes in the parasite due to residence in the host*

a. Immunology. Residence in a host may bring about the building up of an active, acquired resistance on the part of the parasite in certain cases. The well-known hypothesis of Welch (1902), that bacteria are stimulated to protect themselves by the production of antibodies when they are subjected to the defensive forces of the host, no doubt holds true for protozoa. That this should occur is not at all strange since parasites are living organisms and doubtless react to various stimuli much as does the host. Not only are parasites supposed to actively protect themselves from the host, but they appear to be capable of modifications that enable them to resist harmful therapeutic agents. Thus races of parasites are supposed to develop that are "fast" to substances ordinarily destructive. For example, it is customary to speak of arsenic fastness in trypanosomes and quinine fastness in malarial organisms. If trypanosomes are subjected to a dose of an arsenical insufficient to destroy them, they become more resistant to arsenic than they were at the beginning. Repeated doses increase the resistance. That this result is not due simply to the selecting out of more resistant natural strains is indicated by the fact that Oehler (1913) obtained a resistant strain in a pure line infection. The resistance may persist for a long time, e.g., after passage through 400 animals, during which many thousands of asexual generations must have occurred. Loss of this resistance may follow passage through a different species of laboratory animal or through the invertebrate host.

b. Aggressivity. The term aggressivity is applied to the invasive powers of a parasite. Changes in parasite aggressivity seem to occur due to residence within a host and may be illustrated by several examples. Epidemics of malaria have been described occurring in endemic regions. No one has satisfactorily explained this phenomenon. Parasites that were extra-virulent may have been

brought in from some other region, or the resistance of the general population may have decreased all at once thus enabling the organisms already present to undergo rapid increase in numbers, but it is possible that these epidemics are due to an increase in the invasive powers of the organisms responsible for the endemic malaria of the region.

Differences in invasive powers have been noted among the cysts of the dysentery amoeba, *Endamoeba histolytica*, which may have been due to changes during residence in the human host. For example, Baetjer and Sellards (1914) state that "chronic cases of long standing, with mild symptoms, often produced an attack in animals which was of comparatively short duration and eventually ended in recovery;" and Wagener and Thomson (1924) were able to infect kittens without difficulty with amoebae from an acute case of amoebiasis, but succeeded in only one of fourteen kittens when amoebae were used from a chronic case of amoebiasis. The supposition is that the conditions of chronicity modified the aggressivity of the amoebae until a strain with very little invasive powers was developed.

8. Host parasite adjustments during an infection

a. Carriers. During the course of a natural infection as outlined above various adjustments occur between host and parasite. Continued reproduction by the parasite without check would obviously result in the death of the host; this would be a disadvantage to the parasite, since it is thus prevented from further growth and multiplication and especially from dissemination. Spontaneous recovery results in most cases of protozoan infection, but by recovery is meant the cessation of symptoms and not the total disappearance of parasites from the body. Frequently the host by means of its acquired resistance is able to destroy most but not all of the parasites, and hence to bring about the carrier condition.

A carrier is a host in which parasites live and by which they are disseminated but exhibits no visible symptoms of infection. Walker and Sellards (1913) distinguished two types of carriers in their work with human amoebae, (1) contact carriers who are parasitized but never have exhibited symptoms, and (2) convalescent carriers who have recovered from the disease but are still infected. This is the ideal condition for the parasite since it is not in danger of losing its host and is ensured of the distribution of its offspring. As a matter of fact most host-parasite relationships are of this type; hosts become infected but never show symptoms and are apparently none the worse because of the presence of the parasite, a sort of equilibrium between host and parasite being established. Certain species of hosts are almost universally infected by certain species of parasites in nature and the parasitized condition might almost be considered the normal state for these species.

Infection without symptoms is supposed to be the result of long periods of association. According to this view the length of parasitism of a certain species of host by a certain species of parasite can be determined approximately by the host-parasite reactions. For example, if a parasite is pathogenic and lethal for a certain host the association is supposed to be recently acquired whereas the absence of symptoms indicates a long period of consociation. Frequently carriers are spoken of as reservoirs since they are store houses for the organisms that are responsible for the spread of the parasite to new hosts. In certain cases the para-

site is infective both to man and to lower animals and one or both kinds of hosts may serve as reservoirs. Very little is known at present regarding the conditions underlying the carrier state.

b. Latency. Similar in certain respects to the carrier condition is the state known as latency. When parasites are present in a host but do not make themselves manifest, they are said to be latent. Latency, however, does not necessarily require the dissemination of the parasites by the host. In some cases a host may be parasitized and show no symptoms; in other cases a host may recover from symptoms but still harbor parasites; both types of conditions may be included under the term latency. Certain changes in host or parasite may bring on symptoms in a host that had never previously exhibited evidences of infection; such a case might be considered one with an extended incubation period.

c. Relapse. Symptoms may appear in a host that had previously shown symptoms but had apparently recovered; such a reappearance of symptoms is known as a relapse if the latent period is short and a recurrence if the latent period is long. Relapses may be induced in certain infections by definite stimuli but the physiological bases for this have not been determined.

Perhaps the host-parasite relationship resulting in the carrier condition, latency and relapse may best be illustrated by facts derived from the study of malaria in man and birds. Relapse is in certain respects the most important phase of malaria, since it is largely responsible for the maintenance of the race from year to year. For example, the malarial organism does not pass the winter in the mosquito in our Southern States but lives during this period only in man. In the spring human carriers have relapses, numerous gametocytes (fig. 26c, 27c, 28c) appear in their blood and from them the mosquitoes become infected. If relapse could be prevented the mosquitoes would have no chance of becoming infected and malaria would soon die out.

Many cases have been described of primary latency in malaria, i.e., the appearance of symptoms months or years after infection, although the normal incubation period is three weeks or less. In these cases parasites had no doubt been present in small numbers but unable, because of some sort of host resistance, to increase sufficiently to cause symptoms until a change took place in the physiological state of the host which broke down this resistance. During the normal course of a malarial infection the parasite number rises to the peak then falls, and finally becomes so small that no parasites are to be found in the blood when examined by routine methods. Symptoms cease as the parasite number falls. Frequently parasites appear again in large numbers and symptoms are again experienced after an interval of a few days or weeks, showing that not all of the parasites were destroyed at the end of the primary attack.

Various theories have been advanced to account for such cases of relapse. The theory with most evidence in its favor is that proposed by Ross. According to this a few parasites remain in the host after symptoms cease, and these are able to maintain the race by asexual reproduction. Work done in this laboratory with bird malaria seems to prove the correctness of this theory. Dr. Ben-Harel (1923) showed that during the period between the cessation of symptoms and the appearance of a relapse, malarial organisms are present in the internal organs undergoing asexual reproduction. Dr. Lucy G. Taliaferro (1925) further proved

that asexual reproduction during this period continues at the same rate as during the period of symptoms. The conclusion is that the rate of reproduction is not changed, but most of the offspring must be destroyed in some way at present unknown. If the physiological state of the body is changed these parasites are not destroyed as fast as they are produced and a relapse ensues. The subcutaneous or intra-muscular injection of various substances called provocatives is capable of bringing about this result. Some of these are adrenalin, ergotin, salvarsan, and strychnin. Relapse may also be brought about by radiation with ultraviolet light (Whitmore, 1923) and frequently results from exposure to cold or sun, from inebriation, errors in diet, surgical operations, etc. It seems probable that these various stimuli cause some change in the blood favorable to the parasite, such as an increase in sugar content; experiments are now in progress to test this hypothesis.

9 *Therapeutics*

Host-parasite relationships may be profoundly modified by treating the host. This may take the form of building up the resistance of the host (biological therapy) or of destroying the parasite either directly or through the host (chemical therapy).

a. Biological therapy. Constitutional biological therapy involves the usual procedures for maintaining or increasing natural host resistance, such as rest, minimum movement, and the treatment of other infections when present. Often the host may be aided by a certain type of nourishment. For example, a milk diet is prescribed in cases of intestinal amoebiasis since milk produces a small amount of putrefaction and is practically all absorbed before it reaches the large intestine where the amoebic ulcers are located.

Vaccines, antitoxins, etc., that increase the active resistance of the host are not available for protozoan diseases. There seem, however, to be no insurmountable obstacles to their preparation and use. A close approach to vaccination is the custom reported to have been prevalent among the Jews of Bagdad who infected their children with the organism of oriental sore (*Leishmania tropica*, fig. 22) by direct inoculation since they had learned that one attack gave immunity to further attacks; it was thus possible to infect unexposed parts of the body and avoid sores that might otherwise appear on the face.

An interesting zootoxin was obtained by Pfeiffer (1891) from *Sarcocystis tenella*, a sporozoan muscle parasite of sheep which Laveran and Mesnil (1909) named sarcocystin. This substance is highly toxic and 0.0001 gram per kilo of body weight is fatal to rabbits. Teichmann and Braun (1911) by immunizing rabbits obtained an effective antitoxin and McGowan (1913) found that the serum of infected sheep gave positive complement fixation.

b. Chemotherapy. Drugs may be used to aid the host either as parasiticides by destroying the parasites or as agents for building up host resistance. In many cases it is difficult to determine which of these processes is taking place. There seems to be no reason why, in the case of intestinal infections, enemas containing drugs toxic to protozoa should not be effective parasiticides. Thus rectal irrigations with a solution of tannic acid or of bihydrochloride of quinine have been recommended in cases of amoebic dysentery, and rectal injections of iodine solution or of methylene blue for flagellate infections. Such treatment might be ef-

ficacious against organisms such as the flagellate *Trichomonas hominis* which lives in the lumen of the large intestine but probably does not destroy organisms such as endamoebae and coccidia that live in the wall of the intestine. In a similar fashion certain investigators advise vaginal douches with a saturated solution of sodium bicarbonate to destroy the flagellate *Trichomonas vaginalis* (fig. 7), which ordinarily lives in the acid secretions of the vagina.

It seems possible that drugs taken by mouth may act directly upon the parasites within the intestine. *Iodamoeba williamsi* (fig. 4a) is destroyed by the administration of emetine although it lives in the lumen of the intestine. In this case the emetine may kill the parasite by actual contact. Drugs injected into the blood stream may likewise destroy blood inhabiting protozoa.

Progress in the chemotherapy of protozoan infections has been most gratifying within the past two decades. Quinine was already in use in the seventeenth century as a cure for malaria but only recently have satisfactory therapeutic agents for other protozoan diseases been discovered. Emetine was introduced by Sir Leonard Rogers for amoebic dysentery in 1912 and soon came into general use; more recently yatren and stovarsol have both been proven to be specific agents for the cure of this disease. In 1905 Thomas inaugurated the treatment of trypanosomiasis with atoxyl and to this have since been added tartar emetic, tryparsamide, Bayer 205 and Pasteur 309. Tartar emetic which was also found by Vianna (1913) to be efficacious against American leishmaniosis, has been found to be equally valuable for the treatment of kala-azar and oriental sore. No therapeutic agents are yet available for intestinal flagellates and coccidia.

Whether these drugs act directly on the parasite or through the host is still in doubt. In a recent illuminating address Dale (1925) states the situation in the following words. "The conception of a remedy not killing the parasites immediately, but modifying their virulence, or lowering their resistance to the body's natural defences; of a remedy not acting as such, but in virtue of the formation from it in the body of some directly toxic product, either by a modification of its structure or by its union with some tissue constituent; of an affinity of the remedy for certain cells of the host's body, leading to the formation of a depot from which, in long persistent, never dangerous concentration, the curative substance is slowly released; all these conceptions present themselves, again and again, as necessary for our present rationalisation of the effects observed. It can hardly be doubted that they will potently influence the methods by which, in the immediate future, new and still better specific remedies are sought. But though our practical aim, in relation to the affinities of a remedy for the parasite and for the host's tissues, may be radically changed the meaning of these specific affinities, so delicately adjusted to a precise molecular pattern, remains dark."

10. Route taken by parasites in escaping from the host

As already noted, parasites must not only reproduce within the host but their offspring must be able to escape and set up new infections in order to maintain the race. In most cases escape is easy since the parasites attack parts of the host from which natural channels lead to the outside; e.g., intestinal protozoa pass out with the feces. The escape of sufficient trichomonads from the mouth

and vagina to keep these races from dying out is probably brought about by kissing and coitus respectively. The blood-inhabiting protozoa depend upon intermediate bloodsucking hosts for their liberation and dissemination and a truly wonderful series of developmental stages on the part of the parasite and reactions on the part of the host and intermediate host are necessary to accomplish this. The life-cycles of some parasites are so complicated that their survival seems almost impossible.

Other methods of escape are exhibited by protozoan parasites of certain lower animals. Some parasites are set free by the death and decay of the host; others live in an intermediate host that is captured and devoured by the definitive host; some are liberated in the digestive tract of an animal that eats the host, and pass out in its feces; a few species form tumors which break open and allow the parasites to reach the outside; and in some cases the parasites pass from one host to another in the eggs of the intermediate host ("hereditary" transmission).

V. HOST-PARASITE SPECIFICITY

By host-parasite specificity is meant the character of the relationships between species of parasites and species of hosts with respect to host susceptibility and parasite infectivity. Hosts and parasites may be divided into groups and labelled according to their interspecific relations, since observations and experiments have built up a considerable body of facts regarding this subject; but what environmental conditions and host and parasite characteristics are responsible for the facts observed are still very obscure.

1. *Host susceptibility*

Parasitologists have long recognized different types of hosts with respect to their susceptibility to various parasites. Thus if a host is easily parasitized by a certain species it is said to be tolerant, whereas if it is difficult to parasitize it is classed as refractory. A host that is frequently found parasitized by a certain species in nature is known as a natural or autochthonous host; whereas one that does not become so parasitized may be considered a foreign host. If a species of parasite that habitually lives in a certain host species is found in a host that is very seldom infected, that host is spoken of as an accidental or casual host. A host may become infected but throw off the infection after a short time, in which case it is known as a provisional or transitory host; or it may serve as a host for a short stage in the life-cycle of a parasite, thus becoming a temporary host.

Frequently it is possible to infect species of hosts in the laboratory that do not become infected, as a rule, in nature, either because their habits are such that they do not come into proper relations with the parasites or because they are refractory except when large numbers of parasites are present or when these are administered to them in certain definite ways not usually possible in nature. Thus cats are relatively easily infected by laboratory procedure with *Endamoeba histolytica*, the dysentery amoeba of man, but are almost never found to be infected in nature.

Whether or not a susceptible species of animal becomes infected with a particular species of parasite in nature depends primarily on three factors; (1) animal and parasite must live in the same geographical region, (2) the habits of the animal must be such as to bring it into proper relations with the infective stage of the parasite, and (3) the life-cycle of the parasite must be such that its infective

stage is reached when and where the host is available to be parasitized.

The first factor mentioned is so obvious that little discussion is necessary. The absence of certain diseases from certain regions is frequently due not to the absence of susceptible hosts but to the absence of the parasites. This, for example, may account for the absence of malaria from countries where suceptible human hosts and the proper species of anopheline mosquitoes exist but where the malarial parasites have never been introduced. On the other hand, many cases might be cited of diseases that have appeared in various regions previously free from them because of the introduction of the causative parasite.

The other two factors are really the same considered from the two standpoints of host and parasite respectively. If the life-cycle of a parasite and the activities of its natural host are studied side by side it will appear as though both host and parasite were actually trying to bring about a situation favorable for infection. For example, the gametocytes of the malarial organisms (fig. 26c, 27c, 28c) live in the peripheral blood where they cannot fail to reach the stomach of the mosquito that sucks up the blood; the infective sporozoites congregate in the salivary glands of the mosquito where they seem to lie in wait to be inoculated into a new host. The mosquito lives on the blood of man and thus enables the parasites to enter the blood stream; whereas it might live on fruit juices as it is able to do in the laboratory. The infective mosquito bites usually at night when the host is asleep and is thus able to inoculate the sporozoites successfully during an uninterrupted meal. A change in any one of these conditions might easily bring about the annihilation of the race of parasites; for example, if the gametocytes were localized in the internal organs of man or if the sporozoites did not reach the salivary glands of the mosquito there would be no spread of malaria and the disease would soon die out.

An infection may be acute, malignant, fulminating, chronic or benign, but the evidence does not indicate that the susceptibility of the host to an infection has any bearing on the character of the infection induced. That is to say, a host may be more susceptible to infection, and probably usually is, by a species of parasite that never calls forth symptoms than by a pathogenic or lethal species.

2. *Parasite infectivity*

If a host is easily parasitized by a species, the parasite is said to be highly infective. How much its infectivity is due to the host and how much to the parasite it is impossible to say. Several of the terms noted above with respect to hosts are also commonly used to designate different types of parasites. Thus, we speak of natural parasites, accidental parasites, and provisional, transitory or temporary parasites. Parasites are also classified according to the necessity of existence within a certain host as facultative, when this is not required, and obligate, when the parasite is unable to live in any other host. The invasive powers of a parasite are indicated by such terms as virulent or aggressive and the degree of infectivity with respect to the effects on the host as pathogenic, sublethal, and lethal.

The data regarding some phases of host-parasite relationships in malaria and intestinal protozoa will serve to indicate some of the problems involved in parasite infectivity. (1) The malarial organisms of man can complete their sexual cycle only in the mosquito. Gametocytes of

both sexes may be present in the blood but do not undergo maturation and fertilization as long as they remain there. If an anopheline mosquito of a certain species sucks malarious blood into its stomach the "ripe" gametocytes are stimulated into activity, whereas all the parasites in other stages of the asexual or sexual cycle are destroyed. Maturation, fertilization, the formation of oökinetes, oöcysts, sporoblasts and sporozoites all proceed in regular order and finally fully developed sporozoites congregate in the salivary glands and the mosquito is ready to pass on the infection to a susceptible human host. Not all anopheline mosquitoes are equally capable of infection; many of them are quite refractory and some that appear never to be infected in nature may be parasitized in the laboratory. If mosquitoes of other types, e.g., the common culicines, ingest malarious blood the "ripe" gametocytes as well as all other stages of the parasite are destroyed. The problem here is why are these parasites infective to one species of mosquito and not to a nearly allied species living in the same region and therefore subjected to the same external conditions, and feeding on the same organic material, namely the blood of man or of lower animals. Differences in infectivity are probably due to failure on the part of the gametocytes to resist some agent or agents in the stomach of the refractory host or to the absence *in toto* or in part in that type of host of the agents that stimulate further development.

(2) The intestinal protozoa of man that are transmitted in the cyst or oöcyst stage offer a similar problem. Why do some cysts pass through the entire intestine without apparent change; whereas the cyst walls of others break down and the organisms within are stimulated to develop? Is the difference due to differences in the composition or thickness of the cyst walls or failure of the environment to stimulate activity within the cyst which results in the dissolution of the cyst wall from within? It is evident that factors exist either in the parasite or in the host or in both that account for host susceptibility and parasite infectivity and bring about the conditions that exist in nature, where most parasites seem to be limited to one or a very few species of hosts, being unable to infect other species, usually even those closely allied.

The two extremes of host-parasite specificity may be illustrated by the relations we have found in this laboratory to exist between (1) the giardias of mammals and (2) the herpetomonad flagellates of flies. Within the past few years we have been carrying on a series of investigations (Simon, 1921, 1922; Hegner, 1922, 1923, 1924, 1925) which seem to indicate that the giardias found in each species of host differ specifically from those found in every other species of host and only in a few cases is more than one species of host infected by one species of giardia. Thus morphologically distinct species have been described from tadpoles, house mice and rats, field mice, rabbits, cats, dogs, guinea pigs, and ground squirrels as well as from certain birds and reptiles. Here then is an example of very rigid host-parasite specificity.

In contrast to this are the results of Becker's (1923) studies on the herpetomonad flagellates that live in the intestine of flies. Investigators previous to Becker's work assumed that each species of fly was infected with its own peculiar species of herpetomonad and hence when a new species of fly was found to be infected the organism was given a new specific name. Becker carried on experiments with six species of muscoid flies

belonging to six different genera and found that each species could be infected with herpetomonads from each of the other five species. Because of these results and of the fact that no morphological differences could be observed between the various so-called species, Becker concludes that the flagellates from these six species of flies are all of the same species,—that first described from the house fly, *Musca domestica*, as *Herpetomonas muscae-domesticae*. These results have been confirmed and extended by Drbohlav (1925).

To account for different degrees of host susceptibility and parasite infectivity we must refer again to certain phases of host-parasite relationships already discussed and call attention to several factors not yet mentioned. The most important of these are the natural resistance of the host and parasite, acquired susceptibility of the host, acquired infectivity of the parasite, and changes in the environment within the host. Because of both lack of space and lack of knowledge, only some of the problems will be mentioned here and no attempt will be made to account for the conditions described.

That hosts differ in susceptibility to a given parasite has been abundantly demonstrated. The difference may be racial, familial, or individual, i.e., it may be inherited. It would be interesting to study this subject with hybrids between susceptible and nonsusceptible hosts. Sex and age may also have a profound effect on host-parasite specificity. In general young animals are more susceptible to infection than adults. This was found to be true, for example, by Maxcy (1921) for *Giardia lamblia* in children examined at the Johns Hopkins Hospital.

The physiological state of the host may have an important bearing on its susceptibility. Frequently a refractory host may become infected if his resistance is lowered by overwork, by previous infection with other parasites, by malnutrition, by intoxication, by exposure to wet and cold, by trauma, or by shock. Changes in physiological state no doubt also take place in parasites which raise or lower their powers of infectivity. Other factors that cause no inconvenience to the host may be unfavorable for the parasite. For example, the writer (Hegner 1924, 1925) has called attention to the fact that intestinal protozoa are rarely present in carnivorous animals. He had previously (Hegner, 1923) shown that rats fed throughout their lives on a largely carnivorous diet that was favorable for growth and reproduction were free from intestinal protozoa and that rats heavily infected with intestinal flagellates can be largely freed from their infection, especially with trichomonads, if fed for about a week on such a diet. Presumably rats that are being fed on this diet would not become infected if the parasites were introduced with their food. The change from a largely vegetarian diet to one largely carnivorous brings about great modifications in the bacterial content of the cecum, modifications that the trichomonads are apparently unable to resist.

Opportunities for the study of the effects of the environment upon host susceptibility and parasite infectivity are presented among lower animals with respect to such factors as temperature, diet, starvation, and gas content of the air. Cleveland (1924, 1925, 1926) has carefully studied these factors in the case of termites and their intestinal flagellates. He finds that the four principal species of flagellates of these insects are affected differently by changes in temperature, by starvation and by subjection to oxygen

under pressure. He was able to prove that the termites are unable to live without intestinal flagellates to digest cellulose for them, and that the flagellate *Streblomastix* is not a symbiote but probably receives its nourishment from the other protozoa.

The origin of host-parasite specificity is really synonymous with the evolution of parasitism. It is obvious, as already pointed out, that parasitism cannot exist unless the hosts and parasites involved are present in the same region and behave in such a way as to come frequently into contact. If these conditions are fulfilled, the factors that make it possible for the parasite to live and reproduce within the host present themselves for consideration. Thus it seems certain that man often takes in with his food the infective stages of many parasites of lower animals, e.g., the cysts of giardias of rats and mice, and the oöcysts of coccidia of cats, dogs and rabbits; and that his blood stream is inoculated frequently by culicine mosquitoes with the organisms of bird malaria. These organisms are not able to remain in the body of man because man does not tolerate them.

But what factors are responsible for tolerance or refractoriness and how have these conditions arisen in the course of evolution? Some of the factors involved have been discussed above and, as we have seen, are still very obscure. Our account has been based on the conditions of host and parasite as we find them today without much consideration of how the present status has been reached. There can be little doubt, however, but that long association has brought about changes in both host and parasite which make it possible for them to live together in harmony except under special conditions. An increase in the virulence of the parasites might disturb the equilibrium established and bring about pathological conditions in the host; a decrease in the resistance of the host might have the same effect; or a decrease in the aggressivity of the parasite might prevent infection; and an increase in the resistance of the host might also prevent infection.

VI. CONCLUSION

In conclusion a few remarks may not be out of place regarding the scientific and practical importance of investigations of host-parasite relationships. Biologists interested in this field are searching for the truth without special attention to its effect upon human welfare. They will be satisfied only when all the various phases of the subject have been made clear. New data reveal new problems and the program is thus undergoing constant modification. There is no fear of exhausting the subject, since each step in advance brings us closer to the fundamental problems of life and discloses new and ever more fascinating questions to be solved.

No special section of our program is devoted to the practical aspects of host-parasite relationships. These, however, are always kept in mind and any new data obtained are always scrutinized for possible applications to prevention and control. Our investigations are of importance from the standpoint of personal hygiene since they furnish the knowledge necessary to protect the individual from protozoan infections. Of even greater significance are the data of use to workers in the field of public health since whole communities may be protected as a result of these scientific investigations.

Finally there is always before us the possibility of throwing light on the greatest of all of our problems, that of

the origin and evolution of parasitism. The materials available for observation and experiment are particularly favorable for attacks on this problem, and as an added incentive is the knowledge that the elucidation of the changes that occur during the development of the parasitic from the free-living habit may furnish the key to the solution of the problem of the method of evolution.

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THE MATURATION DIVISIONS IN RELATION TO THE SEGREGATION OF HOMOLOGOUS CHROMOSOMES

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I. INTRODUCTION

THE discovery of new facts and their correlations with each other and with those previously known may satisfy the individual research worker, but the practical applications of the facts hold the chief interest for those in other fields of endeavor. Thus, cytology principally interests the public on account of its relation to pathology, to physiology, and to evolution and heredity. Its relationship to the last of these is the especial concern of the present paper.

Living things, plant or animal, are either single cells as in the lower forms of life or coördinated groups of many cells as in all higher organisms. In other words, the unit of living matter is the cell. This is a microscopical bit of protoplasm which contains a highly specialized, centrally-located part called the nucleus. The essential constituent of the nucleus is a substance which stains deeply with basic dyes, hence Flemming ('79) named it chromatin from the Greek word χρωμα meaning color. Concordant evidence from many lines of work has been sufficient to convince most biologists that chromatin, which is the only material contributed in equal amount by both parents in fertilization, is the physical basis of heredity. The chromatin is in a loose, spongy condition during the ordinary processes of metabolism, but condenses when a cell prepares to divide. It then becomes evident that there is a definite number of dense bodies which were named chromosomes by Waldeyer in 1888. During division each chromosome splits lengthwise and a half of every one goes to either new cell.

Each species has a definite chromosomal complex, the characteristics of which are most readily distinguished just before the halves of the chromosomes separate during cell division. For instance, the number of chromosomes is practically constant, although certain exceptions exist due to the sex-determining mechanism, supernumeraries and multiple formation. Also a graded size series is usually present. This series is actually double as there are almost invariably two of a given size and shape. Of these two morphologically alike, paired or homologous chromosomes, one has been derived from the male and the other from the female parent.

The germ cells in preparation for fertilization undergo a series of changes called collectively gametogenesis. The part of this process with which we are particularly concerned is called maturation and consists of two cell divisions of a somewhat special type. These are known as the first and second maturation divisions. The behavior of the pairs of chromosomes during these two divisions is the especial field of this paper.

Before the maturation divisions, homol-

ogous chromosomes conjugate. Each member has already split longitudinally as for an ordinary division so that the result is a chromosome called a tetrad, composed of four parts or chromatids, which may or may not be distinguishable entities. At the first maturation division every first spermatocyte, or oöcyte, as the case may be, gives rise to two cells, each of which contains the same number of chromosomes as its parent cell, but instead of four parts, each chromosome now has two, and is called a dyad. At the second maturation division in the male both of the cells derived from one first spermatocyte divide, giving four cells (spermatids) in all. Each of these cells contains one chromatid from every tetrad; e.g., if a first spermatocyte had 11 tetrad chromosomes, each of the four spermatids to which it gave rise would have 11 chromosomes but every one of the latter would be a single chromatid or monad, as they are now called. The oöcyte goes through a similar process but only one functional egg is formed, as three of the cells are abortive. In either case the germ cells become haploid, that is, they contain a single series of chromosomes. The union of the two mature germ cells to form a new individual restores the full, or diploid, number of chromosomes. Thus the initial reduction in number of chromosomes occurs through the union (synapsis) of homologous or like chromosomes, one contributed by the egg and one by the sperm, and not as a result of cell division. This process is known as pseudo- or false reduction, since the actual distribution to different cells is accomplished by the two following divisions.

The question of interest is—Which division separates the part of a tetrad derived from one parent from that derived from the other? Obviously, there are several possibilities. The synapsed pairs may separate at the first division; one-half of each may go into either second gametocyte to be separated at the second division; or, it may be a matter of chance whether the dyads which separate at the first maturation division are derived from the same or opposite parents. Do all of the tetrads of a species follow a given procedure? Or, may the tetrads differ in this respect among themselves? Or, finally, do the homologues of a particular tetrad segregate, for example 90 per cent of the time in one division while those of another tetrad segregate 25 per cent of the time, and if so, what is the cause of this differential behavior? Let us first view the matter from a historical standpoint, then consider the facts presented by recent work.

II. HISTORICAL BACKGROUND

Cytology, in so far as it deals with the chromosomes and heredity, really began in 1883, forty-three years ago, with Van Beneden's discovery that egg and sperm of *Ascaris megalocephala* each contribute one-half of the chromosomes found in the somatic cells of the species. He also saw that this reduction in amount of chromatin in the germ cells occurred at maturation. He assumed that the egg cast out the chromatin which had been brought in by the sperm and the sperm that which it had received from the egg. According to this hypothesis the germ cells alone would be truly male or female and all individuals that resulted from their union would be hermaphrodites. His conclusions have been shown to be erroneous but his observations stand.

In the same year Roux advanced his hypothesis of the linear arrangement of chromatin which is qualitatively different in various regions of the chromosomes.

In 1888 Strasburger reported that Van Beneden's observations applied to a number of flowering plants and a year earlier Flemming, Carnoy and others had shown similar conditions to prevail in other animals.

Flemming ('87) recognized a difference in the appearance of chromosomes in the two maturation divisions. In the second of these he saw that the chromosomes resembled those of an ordinary mitosis, and hence he called it a *homeotypic* division. He also observed that the chromosomes of the first were different and called this division *heterotypic*. Unfortunately, most of the later writers have considered the heterotypic and reduction divisions as synonymous. Flemming's description did not involve this association but it has become so firmly established as to render the use of the terms heterotypic and homeotypic undesirable.

As a matter of fact the chromosomes of the second maturation division resemble those of an ordinary mitosis because they are identical in structure. In each case, a chromosome at metaphase is composed of two similar parts or chromatids. The chromosomes at the first maturation division, on the other hand, are actually composed of four similar parts or chromatids, whether or not they are visible, hence the appearance is different. The two chromatids which go to each cell at the first division may be derived from different parents or may be each one-half of a parental chromosome: as will be shown later, unless there is a morphological or physiological difference between the homologues it is impossible to determine which is the case.

Weismann in 1887, in an essay based on Roux's work of 1883, put forward what is now known as the Roux-Weismann hypothesis which holds: (1) the chromatin is the physical basis of heredity; (2) it is differentially organized; and (3) the differentiated units are linearly arranged. In order to maintain a constant number of "ids," Weismann saw that reduction of number must occur before fertilization; otherwise, the number would be doubled at each generation. He predicted that reduction would be found to occur during maturation and that one of the divisions would be distinguishable in form from the other. He suggested two ways in which this reduction might occur, either by a sorting out of chromosomes into two similar groups, one of which would go to each pole without division of the constituent chromosomes, or by a transverse instead of a longitudinal division of each individual chromosome. For the intrinsic process, whatever the method, he proposed the term *reduction division*. The ordinary longitudinal division was already known as an *equation division*.

This paper appeared simultaneously with that of Flemming in which he described the first maturation division as heterotypical.

We have then these facts established; (1) the body cells and unripe germ cells of most organisms contain twice as many chromosomes as the mature germ cells; (2) the reduction in number is effected during maturation, and (3) the diploid number is restored by the union of the germ cells to form a new individual. The foregoing presupposes that the chromosomes are self-perpetuating bodies which grow and reproduce themselves, but never lose their individuality although, of course, they may change their appearance.

Van Beneden's report ('83) that egg and sperm of *Ascaris megalocephala* each contribute one half of the chromosomes which are present in the cells of the early embryo contained the inherent idea of a

persistent individuality. Rabl ('85) was the first, however, to definitely study the chromatin in its diffused condition in order to determine the behavior of the chromosomes in the formation of the so-called nuclear network. He concluded that the chromosomes preserve not only their identity but largely the grouping which they had at the end of the preceding division. While the chromosomes do form fine anastomosing branches which give the appearance of a network, critical study of the conformation of such a nucleus revealed the areas occupied by individual chromosomes and that during condensation the chromatic substance contracted and the chromosomes assumed definite form again in approximately the same position which they had occupied at the beginning of the process. Rabl's paper was based on his study of the body cells of *Salamandra maculata* (Rabl) and still deserves to rank as a masterpiece of early cytological literature along with those of Flemming, Van Beneden and Boveri. However, the clean cut and persistent work of Boveri, from 1888 on for a number of years, did most to establish the concept of chromosome individuality. Thus the foundation for the chromosome theory of heredity was laid within the five year period from 1883 to 1888.

Much of the work since has been concerned with the manner and time of reduction. Almost every conceivable mechanism has been sponsored at one time or another. According to Weismann's hypothesis each chromosome was composed of ids, and each id contained determiners for the sum of all the characters of the organism. The chromosomes, therefore, would differ from one another only in so far as there was variation in a species since they would represent different lines of ancestral germ-plasm. Even many of the early cytologists agreed with this view that the chromosomes were essentially alike both qualitatively and quantitatively.

III. MORPHOLOGICAL AND PHYSIOLOGICAL DIFFERENCES BETWEEN CHROMOSOMES DEMONSTRATED

Three papers which appeared in 1901 and 1902 undermined this view. Two of these, one by Boveri and the other by McClung, strongly indicated functional differences. The other by Sutton clearly demonstrated morphological distinctions.

Boveri studied the larvae of sea-urchins in which the normal combination of chromosomes had been altered by means of double fertilization. He found 36 chromosomes in the normally fertilized eggs of the species with which he worked, 18 of which were contributed by each parent. Eggs which had received two sperm had another set of 18, which gave 54 chromosomes. When these had split for the first cleavage there were 108. Double fertilized eggs usually formed four, or occasionally three, cells (blastomeres) at the first cleavage. If the chromosomes happened to be distributed equally in the case of four cells each would receive 27, which would be less than the normal number, 36. As a matter of fact they were not distributed equally. Some cells received more than 36, others correspondingly less. Normal embryos appeared very rarely. As Boveri knew from experiments with enucleate fragments of egg and artificial parthenogenesis that the reduced set of chromosomes contributed by the sperm or egg alone was sufficient to cause normal development, he concluded that each blastomere formed by the first cleavage of these "normal" larvae had received at least one complete haploid set. In such larvae all of the parts were present and fully developed but different thirds

or fourths showed individual variations which normally could be found only in different specimens. Ordinarily the plutei were not normal but the different thirds or fourths could be recognized as coming from a given one of the original blastomeres. One part would be normal for example, as regards skeletal development, while others would lack any trace of a skeleton. Furthermore, it was known that the first four cells formed by cleavage might be separated from each other and that such isolated blastomeres from a normally fertilized egg developed exactly alike while those from a doubly fertilized egg very rarely did.

From these facts Boveri concluded, to translate literally, that: Not a given number but a given combination of chromosomes is necessary for normal development and that this can mean nothing else than that the individual chromosomes must possess different qualities.

McClung had previously reported the occurrence in the Orthoptera of one chromosome, called the accessory, which differed from the others during spermatogenesis both in behavior and in distribution in such a manner that half of the mature sperm possessed and half lacked this chromosome. In 1901 he put forward his hypothesis that this chromosome was a sex-determinant and thus for the first time suggested an association between a particular chromosome and a particular character or group of characters.

Shortly afterward Sutton ('02) published his critical analysis of the morphological characters of the chromosome group of the short-horned grasshopper, *Brachystola magna*. He showed that the diploid group of twenty-three was made up of two morphologically equivalent size series of eleven members each with one additional chromosome, the accessory. There were six smaller chromosomes and seventeen larger ones; but except for the accessory there were always two of a size. In the first spermatocyte, he found that each two of a given size had united so that the haploid number of chromosomes formed a single size series. The six small ones had paired to form three small tetrads; likewise, sixteen of the larger ones had united in pairs, leaving the accessory without a mate. In the second spermatocyte, where the chromosomes again were dyads as in the spermatogonia he readily recognized a single haploid series directly comparable to either of the size series of the spermatogonia. As this was the last division before fertilization and the egg was known to undergo a similar process, Sutton readily concluded that the other size series was contributed by the egg.

As his final suggestion in this paper Sutton wrote: "I may finally call attention to the probability that the association of paternal and maternal chromosomes in pairs and their subsequent separation during the reduction division as indicated above may constitute the physical basis of the Mendelian law of heredity"; this view he elaborated a year later and it has since received support from many lines of work.

These three contributions by Boveri, McClung and Sutton firmly establish the concept that the chromosomes differ both quantitatively and qualitatively.

IV. GENETICAL EVIDENCE OF QUALITATIVE AND QUANTITATIVE DIFFERENCES BETWEEN CHROMOSOMES

The confirmation of these views by combined genetical and cytological studies is too well known to need much discussion. Two of the best known instances of such correlated studies are those on the fruit-fly, *Drosophila*, by Morgan and his group at Columbia, and on the

jimson weed, *Datura*, by Blakeslee and Belling at Cold Spring Harbor.

In *Drosophila melanogaster* the diploid chromosomal complex consists of two large pairs, one small pair and the sex chromosomes, xy in the male and xx in the female. From genetical studies the behavior in heredity of some hundreds of characters is known. These characters fall into four groups, a large one which is sex-linked and where the characters follow the same sort of distribution as the sex chromosomes, one small group known to be associated with the small pair and two large non-sex-linked groups which correspond to the two large pairs.

In the jimson weeds, the haploid complex consists of twelve chromosomes, but Blakeslee and Belling have obtained plants which instead of being diploid are triploid; that is, they have three complete sets of chromosomes. During maturation two of the three chromosomes of a set go to one pole and one to the other, the distribution of the different sets taking place at random. The gametes, therefore, contain various different combinations, so that on recombination during fertilization it is possible to get various assortments. By patient work, Blakeslee, Belling and their associates have sorted out twelve mutants, each of which has a different set of chromosomes in the triploid condition, while the other chromosomes are present in the normal diploid sets. It is possible to know their chromosomal constitution from a superficial study of these mature plants.

V. OPPONENTS OF THE CHROMOSOME THEORY OF HEREDITY AND THEIR THEORIES

Notwithstanding such clear cut support for the chromosome theory of heredity, a certain group of workers have been ready to take the opposite side of the argument; that is, they are sceptical as to the chromosomes preserving their individuality from one cell generation to another or even having individuality at any time. Likewise, they are not willing to grant that the chromatin is the physical basis of heredity. Meves, Fick and Della Valle are among the leading opponents of the chromosome theory of heredity and their views may be mentioned briefly.

Meves ('96, '11) holds that each species inherits the capacity to produce a given number of chromosomes from the chromatin of the resting nucleus of the body cells and to form half that number in the germ cells at maturation, just as it inherits the ability to develop other characters belonging to the species.

According to Della Valle ('11), the chromosomes arise *de novo* from the resting nucleus after the manner of the formation of liquid crystals, their size being due to a physico-chemical quality of the chromatin and their numbers to the quantity of chromatin present. This theory does not account for the fact that the chromosomes, at their maximum density within the cell, attain various sizes in most species, nor does it explain why the gametocytes, the nuclei of which are much larger than any others in the body, should have only half as many chromosomes.

Fick ('05) has a similar conception which he has advanced as the "Manoeuverian hypothesis;" he claims that the chromosomes which appear at each cell division are *de novo* "tactical formations" of the chromatin comparable to the manoeuvers of a military body. The force which is assumed to direct these manoeuvers is again a physico-chemical one.

The objection to such hypotheses is that they do not fit the facts. For a discussion of the subject the reader is referred to papers by Wilson ('09, '10), McClung ('17), and Parmenter ('19).

VI. VARIOUS THEORIES AS TO SYNAPSIS AND SEGREGATION OF HOMOLOGOUS CHROMOSOMES

Let us return to a consideration of the work of those who regarded the chromosomes as persistent and self-perpetuating physical entities.

Rückert ('92) and others held that the chromosomes before any cell division, greatly elongated into fine, coiled threads which became associated end-to-end to form a continuous spireme. In the case of ordinary cell division this spireme segmented into the diploid number of chromosomes, but at the time of maturation it segmented into the haploid number. During the first maturation division, the chromosomes were supposed to divide in the same manner as in the body cells, i.e., by means of a longitudinal split. The second division was held to be transverse so as to reduce the number of different ancestral germ-plasms, used in Weismann's sense. Weismann himself expected reduction to occur at the second maturation division because the diploid number of chromosomes was known to be present in certain parthenogenetic eggs which form but one polar body.

O. Hertwig ('90), Boveri ('89), and Brauer ('93), were among the first to report that the chromosomes are split twice longitudinally as they enter the maturation divisions. For this reason they at first denied the existence of a reduction division which, under the conception of the time, seemed to involve a transverse division. However, the work of Winiwarter ('00), the Schreiners ('06) and others made it apparent that only one of the spaces was due to a split, while the other was the space between the members of a pair that were associated side-by-side instead of end-to-end. Thus, they clearly showed that a reduction division in Weismann's sense would be one which separated the parts derived from different parents.

Some assumed that two separate spiremes were formed, each by the end-to-end union of the chromosomes derived from a given parent. These spiremes first split, then conjugated side-by-side, and finally discontinued the end-to-end association so as to leave the haploid number of chromosomes (tetrads); the four parts of each of these were separated longitudinally in planes at right angles to each other. Others, chiefly Vejdovsky ('07) and Bonnevie ('08) believe that the chromosomes completely fuse longitudinally and that the resulting body then splits twice lengthwise so as to give four equal parts which, however, are not comparable to the halves of the conjugating chromosomes.

The view most generally held at present is that no continuous spireme is formed but that the homologous chromosomes unite. According to some, the association is end-to-end (telosynapsis); to others, side-by-side (parasynapsis). While both types of synapsis may exist it is significant that parasynapsis has usually been reported wherever the stages which directly follow the last spermatogonial or oögonial anaphase have been studied in detail from favorable material.

A. and K. E. Schreiner ('06) presented the first convincing support of this view in their work on the annelid, *Tomopterus*. Wenrich ('16) published one of the most authoritative pieces of evidence for parasynapsis. In *Phrynotettix magnus*, a short-horned grasshopper, he was able to trace three well marked pairs of chromosomes from the spermatogonia through the growth period to the first maturation division.

Both McClung and Robertson were at first led to favor telosynapsis by their

studies of prophases of the first spermatocytes of short-horned grasshoppers, but changed their views when they carried their studies back to the more difficult stages which immediately follow the last spermatogonial division.

Among the most ardent advocates of an end-to-end union today are the *Oenothera* cytologists, Davis, Gates and Cleland. In every figure which they have published it is granted that dyads are in end-to-end union; but these figures all represent stages which just precede the first maturation division—and this is exactly the phase which at first led McClung and other competent cytologists to favor telosynapsis, even in a group as exceptionally favorable for cytological work as the grasshoppers. There is not one satisfactory figure of the stages which immediately follow the last pre-maturation division.

On the other hand, since 1904 Gregoire has consistently argued for parasynapsis in the flowering plants, and no case of telosynapsis can be considered as satisfactorily demonstrated by studies on material fixed in such a manner as to give the artificial clumping of chromatin in a more or less solid mass at one side of the nucleus, known as synizesis. Such a fixation renders it impossible to study the very stages at which parasynapsis would be expected to occur. The later end-to-end association may be only the final stage of disunion between chromosomes which were originally synapsed side-by-side.

Both types of synapsis may occur, but as we shall see presently, the question of the occurrence of either type is immaterial in a determination of time of segregation. In the meanwhile, let us orient ourselves by consideration of some general questions.

VII. GENERAL QUESTIONS INVOLVED

In the first place, what is the object of synapsis? The purpose which first appealed to me as self-evident is fully expressed by the following quotation from one of Sutton's papers ('02, p. 39); "There is, therefore, in *Brachystola* no qualitative division of chromosomes but only a separation of the two members of a pair . . . . by the light of this conception we are enabled to see an explanation of that hitherto problematical process, synapsis, in the provision which it makes that the two chromosomes representing the same specific characters shall in no case enter the nucleus of a single sperm or mature egg." This still seems to me the basic necessity back of synapsis. The phenomenon known as crossing-over occurs during the process, either by means of chiasmatypie or otherwise, but this, in my opinion, is an incidental result rather than a fundamental purpose.

The next question which logically presents itself concerns the necessity for two maturation divisions; if the preceding assumption is correct, one would evidently be sufficient for the purpose of segregation. I would suggest that the occurrence of an extra division is perhaps simpler than an alteration in the very mechanism of division. At a given stage of mitosis, probably the telophase, the chromosomes normally split in anticipation of the next division with the result that each member of a pair is already split before they synapse. It would seem that this normal split would have to be suppressed or two divisions must take place to distribute the four parts present after synapsis. On the basis of this explanation, another split might be expected during the telophase of the first maturation division. However, the chromosomes are already dyads

and this condition may be sufficient to inhibit a further splitting.

Finally, we may be asked why we are concerned as to which division separates homologues, especially since the two divisions distribute each of the four chromatids of a tetrad to different germ cells. For a dyed-in-the-wool scientist, a satisfactory answer is that we desire to know the truth. For those who have never known the thrill of establishing a scientific fact, there is also a sufficient answer. Since the chromatin is now generally accepted as being the physical basis of heredity, it is clearly desirable to determine as accurately as may be its behavior during maturation and fertilization since only with accurate knowledge of the usual behavior is it possible to detect variations which may be, in part, the mechanism of evolution, and to determine experimentally, if not the causes which operate in nature, at least others which will produce effects. Among the more drastic measures with which the laboratory worker is inclined to experiment may be mentioned radium, X-rays and alcohol. Others which approach nearer the experiments of nature seem to me to be more likely to render significant results. Chief among these is an enforced change of food habit, such as a drought or accidental landing in a new habitat might cause. In the light of our present knowledge of various vitamines, calcium metabolism, etc., this seems one of the most promising lines of work. Experiments with extremes of humidity and temperature may also be expected to yield results.

Any cause which will produce an effect on the chromatin of the germ cells such as a permanent multiple association, a shift of spindle fiber, or a change in the size of a chromosome (all of which are known) or some less tangible effect which may cause segregation at one division rather than another may be expected to produce physiological as well as morphological changes. If these are produced for a single season in any considerable portion of a population they will perpetuate themselves provided they are not detrimental, for this is not a question of inheritance in the usual sense, but of actual physical transmission.

VIII. DIRECT EVIDENCE AS TO THE TIME OF SEGREGATION

Let us next consider the facts in regard to the time of segregation. Obviously, given a side-by-side union of morphologically similar, split homologues, it is quite impossible to tell which two of the four threads have come from a given parent. This is especially true because the larger pairs form 8-shaped figures in which the strands are separated two-by-two in planes at right angles to each other in such a manner that the threads which are together in one loop are apart in the next (fig. 1, *A*). Even the smallest tetrads pass through a stage where the four chromatids are arranged in the form of a cross with equal arms (fig. 1, *B*), while some develop modified ring and cross forms (fig. 1, *C* and *D*). Such figures as these are typical of the late prophase preceding the first maturation division in both animals and plants, though they have frequently been misinterpreted. The unprejudiced reader, I am sure, will readily admit that it would not be possible in any of these instances to say which two of the four chromatids of any one of these tetrads has been transmitted by the mother and which two by the father. Yet most cytologists whose work has dealt with these stages have taken sides in favor of either pre-reduction (segregation at the first) or post-reduction (segregation at the second

maturation division). The conclusions in practically every instance have been based on attempts to distinguish between the space which results from a longitudinal cleavage of the chromosomes and that which separates the synapsed members.

As might be expected, the attempt to determine the facts by such uncertain means has not resulted in agreement. Some of the advocates of telosynapsis have favored pre-reduction [notably Montgomery ('01), Farmer and Moore ('05) and the present *Oenothera* cytologists] others post-reduction (see the papers prior to 1912 of McClung, Sutton and Wilson). The adherents of parasynapsis have shown more unanimity in support of pre-reduction [Winiwarter ('00), Gregoire ('07), the Schreiners ('08), Janssens ('09) and Robertson ('16)]. In general they have assumed that the chromatids open out along the space between the homologues more readily than along the plane of the longitudinal cleavage. Such a view might seem logical for forms like that represented at figure 1, *D*, but it is not so convincing when we consider figure 1, *A*, where the chromatids which are together in one loop (*a*) are clearly separate in the next (*b*). Wenrich ('16) was the first to take the position that either pre- or post-reduction may follow parasynapsis.

As already indicated, Wilson and McClung argued for telosynapsis and post-reduction in their earlier papers. Later they became convinced that parasynapsis is at least the most usual method of union and that it is impossible to determine which division is equational and which is reductional from a study of the relations of morphologically similar chromatids.

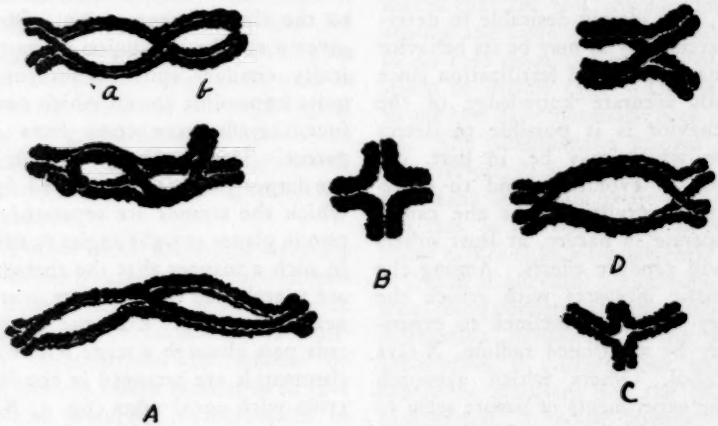

FIG. 1. TYPICAL TETRAD FORMS FOUND IN THE PROPHASE OF THE FIRST MATURATION DIVISION

Note the four parts (chromatids) of each. (From camera lucida drawings of first spermatocyte prophases of three species of grasshoppers.)

Fortunately considerable direct evidence is available from several sources. (1) *Heteromorphic homologues*. Homologues occasionally differ morphologically. In such cases, it is only necessary to obtain individuals in which the members of a pair are heteromorphic and study the distribution of the parts of the resulting

tetrads during the two maturation divisions. (2) *Dyads (except sex-chromosomes) present at first maturation division.* Dyads may be present either as a result of the failure of homologues to conjugate or on account of an upsetting of normal conditions such as occurs in *Datura*. (3) *Sex-chromosomes.* These may be either an X-Y pair, the members of which are morphologically different, an unpaired X or accessory chromosome or a hexad multiple. (4) *Genetical evidence.* In certain species of *Sphaerocarpos* the four spores formed by the division of a spore mother cell remain together at maturity. Allen has demonstrated that the sex determining mechanism is an X-Y pair and has obtained evidence as to the time of segregation in clones derived as above through studies of the mode of inheritance of a pair of characters, the determiners for which are carried by another pair of chromosomes.

(1) *Heteromorphic homologues.* The heteromorphism between homologues so far reported has been of three types: (a) difference in size, (b) difference in point of spindle fiber attachment and (c) difference in contour due to constriction.

(a) The first of these to be reported was a size difference between homologues in three species of short-horned grasshoppers (Carothers, '13). In this group there are twelve pairs of chromosomes in the female and eleven pairs and one without a mate (the accessory or sex-chromosome) in the male. It is customary to number these pairs from one to twelve beginning with the smallest. To date, size differences between homologues have been reported for the first four pairs. The individuals belong to nine genera though it would be possible to greatly extend this number by working over the material in the McClung collection.

My own work, to which reference was just made, dealt with the second pair in one species and the third pair in the other two. Certainly in a vast majority of the cases, segregation occurred at the first maturation division. Robertson ('15) reported a similar condition and behavior in two other species; in one of these, the first pair was involved, in the other the fourth. Neither Robertson nor myself were primarily interested in the time of segregation and it is quite possible, in my own work at least, that occasional segregation at the second division may have been overlooked. However, a later, somewhat hasty review of the slides on which my work was based failed to reveal any case of post-reduction of the members of the unequal pair, so, in table 1, I have recorded these five instances as giving 100 per cent pre-reduction.

Wenrich ('16) in a very detailed study of the spermatogenesis of thirteen specimens of *Phrynotettix magnus*, another short-horned grasshopper, found two small pairs. One, which he designated as "B," had homologues differing in size in eleven out of the thirteen animals. Unlike the five preceding instances, the homologous members always segregated at the second division. The other small pair, which he called "C," was composed of unequal homologues in seven of the thirteen specimens. Furthermore, two types of inequality were present. One type, "C_1," occurred in five individuals and, as in the case of pair "B," the members always segregated at the second division. The other type "C_2," was present in two of the animals and a count of 928 first spermatocyte metaphases chosen at random gave 50.8 per cent pre-reduction and 49.2 per cent post-reduction.

The study of this subject has been extended to species in three other genera

by the writer in a paper ready for press. Certain individuals in all of these have one or both of the two smaller pairs composed of unequal homologues (11 out of 71 *Trimerotropis citrina* for the second pair). *Amphitornus bicolor* gives over 99 per cent post-reduction for the homologues of both pairs. *Mecostethus gracilis* gives 78 to 80 per cent post-reduction for both pairs and correspondingly 20 to 22 per cent pre-reduction. *Trimerotropis citrina* shows 95 per cent pre-reduction for the first pair and 90 per cent post-reduction for the second.

Thus, out of fourteen pairs of chromosomes with homologues which differ in size, six show 95 to 100 per cent pre-reduction, seven 78 to 100 per cent post-reduction, and one 50 per cent pre-reduction and 50 per cent post-reduction. Evidently, segregation occurs with about equal facility at either division, but a given pair in a particular species behaves in a predictable manner.

(b) *Heteromorphism due to shift of spindle fiber attachment.* Chromosomes throughout the plant and animal kingdom are of two types as regards point of spindle fiber attachment and this point shows complete correlation with the shape of the chromosome; i.e., rod-shaped chromosomes have terminal fiber attachment, and V- or J-shaped chromosomes have the fibers inserted at the apex of the bend. Ordinarily, homologous chromosomes have similar points of fiber attach-

TABLE 1

Time of segregation

	1ST PAIR		2ND PAIR		3RD PAIR		4TH PAIR		J TETRADS		HEXADS		ACCESSORY		X–Y	
	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
T. citrina	95	5	10	90												
M. gracilis	20	80	22	78												
A. bicolor	1	99	1	99												
P. magnus c_1	50	50	0	100												
P. magnus c_3	0	100														
A. granulata	100	0														
A. simplex			100	0												
B. magna					100	0										
D. carolina					100	0										
T. parvipennis							100	0								
Trimerotropis									100	0						
Circotettix									100	0						
Mermiria											100	0				
Hesperotettix											100	0				
Anabrus											100	0				
Acrididae													100	0		
Bugs *Anasa*													0	100		
Bugs *Banasa*													100	0		
20 species													100	0		
8 species													0	100		
20 species															100	0
13 species															0	100

ment. The only exceptions, so far reported, are found in certain species confined to two genera of grasshoppers. A combined genetical and cytological study of one of these species, *Circotettix verraculatus* (Carothers, '21), demonstrated that the point of fiber attachment is constant from parent to offspring. In this species, three pairs of chromosomes may be heteromorphic. They are numbers one, seven and eight. Of course, the presence of a heteromorphic pair in one individual presupposes the existence of other individuals in which the homologues would be homomorphic. This becomes clearer on examination of figure 2, which summarizes the results obtained from five matings so far as the three potentially heteromorphic pairs are concerned. The three vertical groups numbered 8, 7 and 1 correspond to the pairs of chromosomes under consideration. The numbers on the left margin indicate the mating. The chromosomes of the male parent are represented on the left of each group, those of the female next, and finally the numbers of male offspring obtained and the various chromosomal recombinations shown by them. If we partly analyze mating number 14, for example, we see that both parents were heteromorphic for the eighth pair. They would both, therefore, form two types of gametes so far as this pair of chromosomes is concerned. In one type it would be present as a rod, in the other as a V. Chance union of these gametes would give the well known Mendelian dihybrid ratio, 1:2:1. The numbers actually obtained, two homomorphic for Vs, six heteromorphic and four homomorphic for rods, approximate this ratio as closely as could be expected from a family of this size. This text-figure is reproduced from my 1921 paper at the cost of some digression since it has a bearing on several points discussed in the present paper. Among these is the persistent identity of chromosomes from parents to offspring, the segregation of the members of a pair into different gametes and their recombination in the offspring according to the laws of chance.

Heteromorphic pairs like these where the difference is one of spindle fiber insertion, always, so far as known, segregate at the first maturation division. I am inclined to think that the reason for this is to be found in the mechanical conditions involved. Certainly it does not follow that when the homologues are homomorphic of either type (Vs or rods) they also segregate at the first division. We have already seen that rod-shaped homologues run the complete scale of possibility as to time of segregation and there is no reason for supposing that those which are V-shaped do not behave in a similar manner.

(c) The third type of heteromorphism mentioned, that due to a constriction, is represented in mating number 2 by one homologue of the seventh pair in the female and is also present in her one male offspring. Such a homologue when associated with either a rod or V-shaped mate always undergoes pre-reduction.

(2) *Dyads (except sex-chromosomes) present at first maturation division.* The unequal homologues of the second pair in *T. citrina* occasionally fail to synapse or else separate so precociously that they lose all orientation in regard to each other by the time of the first maturation metaphase. At all events, they enter this stage not as a tetrad but as two dyads, and their ensuing behavior appears to be purely a matter of chance. They may pass to the same pole or to opposite poles without division: or, either one may divide and the other pass to one pole undivided; giving, in effect, a reduction

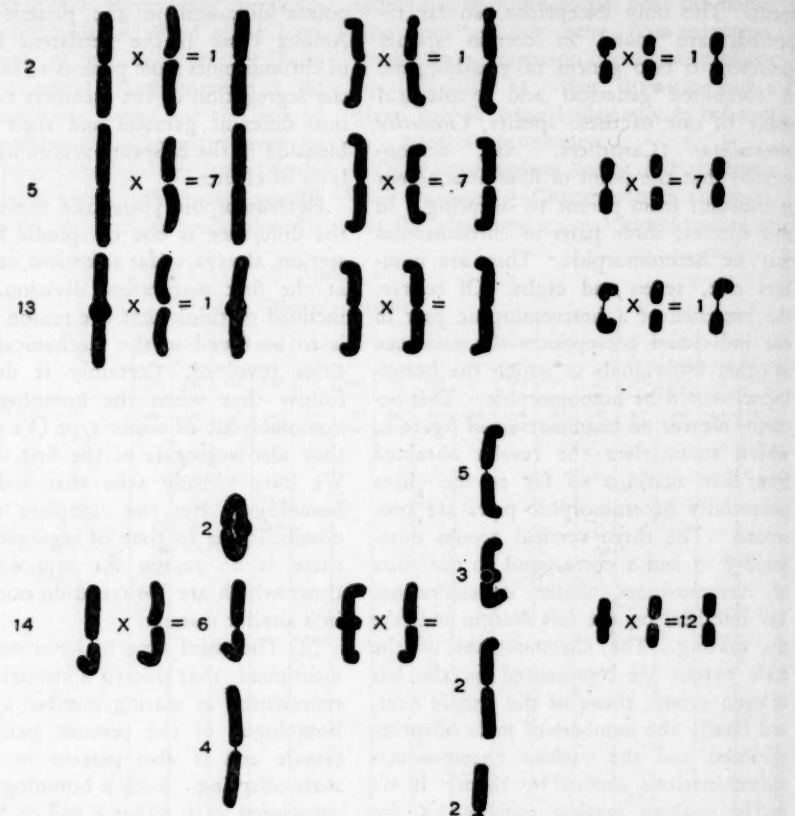

FIG. 2. *Circotettix verruculatus*. A CONDENSED ARRANGEMENT SHOWING THE MORPHOLOGY OF THE THREE CRITICAL PAIRS OF CHROMOSOMES IN THE PARENTS OF EACH OF FIVE MATINGS AND THEIR MALE OFFSPRING WITH THE NUMBER OF INDIVIDUALS IN EACH CLASS

The chromosomes of the male are represented on the left; those of the female on the right. [In mating no. 17, where the form of the chromosomes of the female can only be hypothesized, they are represented in outline.

division for one and an equation division for the other: or, both may divide. In the last case and all others where they enter the second maturation division as monads they do not divide again but simply pass to one pole at random. This erratic behavior lends point to the suggestion made in the earlier part of this article that synapsis is primarily for the purpose of insuring the distribution of one chromatid of every tetrad to each mature germ cell; and it also appears that the two maturation divisions act as a unit process to secure this result, rather than that either one is especially for the purpose of segregation.

On the other hand, in the *Oenothera* and *Datura* mutants where the normal complex has become unbalanced, the extra dyads are reported to segregate uniformly at the first division. To demonstrate that such behavior is invariable would require a rather extensive study.

(3) *Sex-chromosomes.* McClung ('01, '02) put forward a hypothesis of sex-determination which is now generally accepted. The chromosomal mechanism on which this hypothesis was based may be made clear if we consider its operation in the short-horned grasshoppers. The males in this group have twenty-three chromosomes, eleven pairs and the unpaired accessory or sex-determinant. The females have twenty-four chromosomes, twelve pairs. (The accessory has a mate in this sex). After maturation the eggs all contain twelve chromosomes; the sperm on the other hand are of two sorts, one with eleven chromosomes and the other with twelve. The union of one of the latter with an egg results in a complex of twenty-four chromosomes, and the egg develops into a female, while fertilization with a sperm bearing eleven chromosomes gives a group of twenty-three chromosomes, and a male is produced.

At the first maturation division in the male, each of the eleven tetrads divides, the accessory passes into one of the resulting cells without division. In effect this is pre-reduction for the accessory chromosome and results in two types of second spermatocytes, one with eleven dyads and the other with twelve. During the second maturation division each of these cells gives rise to two of its own type except that the chromosomes are now monads instead of dyads.

The hexad multiples are formed by the union of the accessory with one homologue of an ordinary pair and always undergo pre-reduction.

The squash bugs, also, have an unpaired accessory in the male but it divides at the first maturation division along with the tetrads so that all the second spermatocytes are alike. During the second maturation division the dyads separate to form monads but the accessory is already a monad, hence, it passes into one of the daughter cells without division, so that, as in the grasshoppers, two types of sperm are formed but in this instance the accessory undergoes post-reduction.

In many organisms there is a slight modification of this sex-determining mechanism where the accessory has a synaptic mate (Y) in the male. The two are morphologically distinct and are known as the X-Y pair. The end result is again two types of sperm, one bearing Y, which is male-producing, and one bearing X, which is female-producing. The X-Y pair, also, may undergo either pre- or post-reduction. Wilson in his recent book lists forty species, extending from insects to mammals, reported to have an unpaired accessory, which undergoes pre-reduction in thirty-two of the species, and post-reduction in eight, while of thirty-three species having an X–Y pair

pre-reduction is reported for twenty- and post-reduction for thirteen.

The recent work on sex-chromosomes in plants is not yet extensive enough to justify comparisons as to time of segregation.

(4) *Genetical evidence.* Botanical cytologists have stood almost as a unit in favor of pre-reduction; it is, therefore, of especial interest that Allen ('24) was forced by his genetical work on *Sphaerocarpos* to the conclusion that the most reasonable inference from his facts was, "that in some way qualitative segregation can be brought about in both divisions." A clear presentation of his facts would require considerable space and anyone sufficiently interested can acquire them from the original paper.

From the foregoing facts it is evident that neither maturation division can rightly be called a segregation, or reduction, division. The members of a given pair may possess a tendency to segregate at one division in preference to the other, but this is seldom a fixed condition. The two maturation divisions are essentially a unit process and segregation may occur in either.

My hope in presenting this article is (1) that the public may gain a clearer conception of the fundamental principles involved in the process of maturation; (2) that cytological workers will be deterred from making definite statements that either pre- or post-reduction occurs in the material with which they happen to be working unless it is possible to identify the contribution of the two parents for each particular pair of which they speak; and, finally, (3) that teachers will grasp the idea that the maturation divisions are really a unit, and cease to tell the much-abused freshman that one maturation division is for the purpose of segregation and the other is superfluous.

(I am greatly indebted to Dr. H. B. Baker and to Dr. D. H. Wenrich for valuable criticism of this manuscript.)

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ELEVEN THOUSAND GENERATIONS OF PARAMECIUM

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CAN unicellular animals reproduce indefinitely without recourse to fertilization? This was the question to which an answer was sought when the experiment to be summarized was begun nineteen years ago. The consensus of opinion at that time, based chiefly on the work of Bütschli, Maupas, Hertwig, and Calkins, was that fertilization is a *sine qua non* in the life history of the Infusoria (1). The conclusion usually, and I believe rightly, drawn from the data available today, largely from the following experiment, is that fertilization plays no indispensible rôle in the life history of Infusoria when subjected to entirely favorable environmental conditions (2). This conclusion, it may be noted, does not deny that fertilization has a stimulating function.

On May 1st, 1907, a pedigree culture of *Paramecium aurelia* was started with a "wild" individual and has been maintained by the isolation of certain of its progeny practically every day, with the exception noted below. The number of divisions has been recorded at each isolation and has afforded a continuous series of data for the study of the reproductive activity of the culture. Throughout the experiment some of the animals discarded from the lines at the daily isolations have been fixed, stained, and mounted as permanent preparations for the study of the cytological changes during the life history. The culture medium for the first eight months of the work consisted of infusions of hay and fresh grass, but from February, 1908, to the present time various materials collected from ponds, swamps, etc., have been employed. The infusions have invariably been thoroughly boiled to prevent the contamination of the pure culture with foreign strains of *Paramecium*. The possibility of conjugation occurring in the culture has been precluded by the almost daily isolation of the products of division. In short, the animals of the culture today are direct lineal descendants, without fertilization, of the single animal isolated in 1907 (3).

In this manner the pedigree culture was carried for eight years, during which 5071 generations were attained, and then (May 1, 1915), the experiment was considered *formally* closed with the statement that the organisms of the present generation are in as normal morphological and physiological condition as the original individual isolated to initiate the culture. The study has indicated that under favorable environmental conditions the protoplasm of the progenitor of the culture possessed (at least) the potentiality to produce similar cells to the number represented by 2 raised to the 5071st power, or a volume of protoplasm greatly exceeding 10^{1000} times the volume of the Earth. I believe this result indicates beyond question that the protoplasm of a single cell may be self sufficient to reproduce itself indefinitely, under favorable conditions, without recourse to fertilization (4).

However, with this conclusion secure,

TABLE I

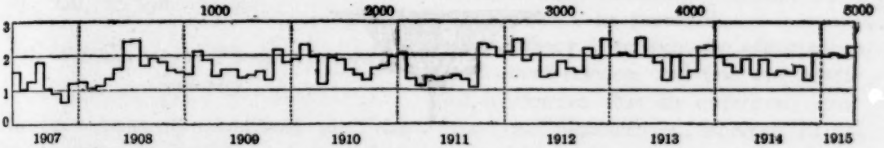
Record of the number of generations attained during each year of the life of the culture from May 1, 1907 to May 1, 1915

YEAR	GENERATIONS	DAILY AVERAGE DIVISION RATE
1	452	1.24
2	690	1.89
3	613	1.68
4	612	1.67
5	662	1.81
6	692	1.89
7	671	1.84
8	679	1.86
Average for 8 years.....	634	1.74

I was reluctant to discard the race and was tempted to keep it under control, but without such exacting daily observation and recording of the daily division rate. Accordingly, it has been kept in this manner up to the present time (April, 1926). But from time to time thirty-day tests have been made of the vitality of the race under the former rigid culture conditions, and in each case the same general average division rate has been revealed as during the first eight years of its life. For example, during December, 1915, 52 generations; during December, 1917, 56 generations; during November, 1920, 54 generations, and during February, 1926, 53 generations were attained. On the basis of such tests it is fair to make the exceedingly conservative estimate of 600 generations attained each year since May 1, 1915. This would give, in round numbers, 11,700 generations attained by the culture during the 19 years of its life, to date since May 1, 1907. The vitality of the culture is further attested by the fact that it is continuously affording animals for various other experimental studies on *Paramecium* at Yale and elsewhere.

Careful studies of the rate of division of sub-lines derived from the main culture and bred under the most constant environmental conditions revealed the fact that there are inherent, *normal*, minor, periodic accelerations and depressions of the fission rate due to some unknown factor in cell phenomena. These were termed rhythms (5). In a search for the underlying factors of rhythms a complicated internal nuclear reorganization process was discovered and named endomixis (6). This process, in essence, consists of a gradual disintegration and absorption of the macronucleus and the formation of a new one from the micronuclear apparatus. This results in the reorganization of the cell (endomixis) without the coöperation of two animals involving syncaryon formation (amphimixis) as in fertilization.

Endomixis obviously introduces an entirely new problem, though, of course, it in no way affects our former conclusion that fertilization, involving syncaryon formation, is not intrinsically a necessary phenomenon in the life history of the organism. Whether endomixis is a necessary factor for the continuance of the race is another question and is now being intensively investigated (7).



GRAPH SHOWING THE RATE OF REPRODUCTION OF THE PEDIGREE RACE OF *Paramecium aurelia* DURING THE FIRST EIGHT YEARS OF CULTURE

The ordinates represent the average daily rate of division of the four lines of the culture, again averaged for each month. The vertical broken lines indicate the limits of the calendar years. The figures 1000, 2000, etc., represent generations and are placed above the periods in which they were attained.

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These two publications contain extended discussions of the problem from different viewpoints.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

A NEW WORD FOR AN OLD THING

Being a review of *Behaviorism* by John B. Watson. New York (People's Institute Publishing Co.), 1925. 6 x 8⅝; viii + 296. $3.00.

By William Morton Wheeler, Harvard University

In this volume, advertised as "the first popular presentation of behaviorism," the author attempts to treat in a series of a dozen lectures, what he seems to regard as a new psychological dispensation which spurted from the intellects of a group of American investigators as recently as 1912. The presentation of scientific matter of such complexity and alleged novelty before a popular audience like that of the People's Institute is an undertaking before which an even more enthusiastic, virile and combative investigator than Watson might quail. And now the old-fashioned psychologists are in tears on account of the bull's behavior and the devastation he has wrought in their china-shop. Both parties are, of course, to blame—the china-shop keepers for setting such store by their fragile, antique wares and their love of exposing them without adequate safeguards, and the bull for smashing them. Perhaps, however, the bull is the less culpable, because the shopkeepers have of late been too enthusiastically convincing him that he is a connoisseur in porcelain.

Psychology is universally admitted to be a queer science, and one can hardly fail to observe that its queerness, apart from the peculiarities inherent in its subjective subject matter, is due in no small measure to the mental peculiarities of its devotees. When we consider that, with very few exceptions, the men who have developed psychological science have been either philosophers, priests or pædagogues, or hybrids of all three, its strangely inhibited, not to say eunuchoidal, aspect is easily understood. To put the matter *crue, nue, verte et sans phrase*, these doctrinaire individuals seem always to have a horror of admitting to themselves and others that they are and will always remain individual mammals of the Family Hominidæ and the Order Primates. Their professions require that they shall give the impression that they subtly vegetate on cloud-banks of ratiocination and pure asexual love and that they possess little or no first hand acquaintance with the instincts, emotions

or appetites, not to mention uglier propensities. Moreover, these are the very castes to whom we consign the education of the young of our species, and the young must, of course, be carefully diverted from all curiosity in their abominable urges and longings. Hence the concentration on the most anæmic psychic processes—consciousness, sensation, perception, apperception, memory, attention, ideation, volition, etc., and the rationalizations, or "thobbing," to use a term recently coined by Henshaw Ward, which compels the psychologist to slur over the real drives of human nature and to pursue his researches and writing, not as a scientist, but as a "*verkappter*" moralist. Pray, what would present day anatomy, physiology and medicine be like if the subject matter of these sciences had been handled by their teachers and investigators in a similar oldmaidish spirit?

After the older generation of psychologists had secreted many tons of literature as dry if not as dead as Tuthankamen's mummy, at the very time when a host of keenly observant novelists were writing the most illuminating studies of individual psychology, the youngsters broke away and are now frisking about in the less arid pastures of advertising and industrial psychology, intelligence testing, behaviorism, "*Gestalt*" and psychoanalysis. And the only excitement the oldsters can get up in self defence is to secrete more literature on such topics as the "Crisis of Psychology," the soul and spiritualism (Driesch) or to admonish the youngsters to behave themselves in the interests of harmony (see the recent addresses of Madison Bentley and Miss Calkins). Of course Watson, as one of the most obstreperous of the youngsters, has been so frequently spanked that he has by this time undoubtedly developed ischial callosities of some thickness. Since henceforth the application of the ferule in the same *locus* would be ineffectual, a more sensitive spot might be sought. To the biologist the whole situation is replete with fun and confusion.

The old definition of psychology as the science of conscious processes being too uninteresting, a new one was sought and found a few years ago by some of the mandarins, who defined it as the "science of behavior." Naturally all the behaviorists at once jumped to the conclusion that they were psychologists. It is not clear, therefore, why Watson and his fellow behaviorists should be castigated for agreeing with the psychologists when they were straining themselves, like many modern theologians, to clothe their old science in more "peppy" habiliments. But Watson may be blamed for his failure to recognize and present behaviorism as a long-established, purely biological discipline. His lack of interest in the history of science has led him to regard himself as the Messiah of a new scientific dispensation dating from the year of grace 1912. Since it must be terribly humiliating to most biologists to feel that they have so long overlooked so promising a path to salvation, a brief historical exegesis may be introduced at this point.

This is Watson's definition of behaviorism:

"Behaviorism, is, then, a natural science that takes the whole field of human adjustments as its own. Its closest scientific companion is physiology. Indeed you may wonder, as we proceed, whether behaviorism can be differentiated from that science. It is different from physiology only in the grouping of its problems, not in fundamentals or in central viewpoint. Physiology is particularly interested in the functioning of parts of

the animal—for example, its digestive system, the circulatory system, the nervous system, the excretory system, the mechanics of neural and muscular response. Behaviorism, on the other hand, while it is intensely interested in all of the functioning of these parts, is intrinsically interested in what the whole animal will do from morning to night and from night to morning."

Now since man is an animal, his behavior must be animal behavior, and the department of biology which deals with this was certainly not inaugurated fourteen years ago. It may be of no particular interest to trace it to Aristotle, but we are justified in regarding Réaumur's work on insects, published during the first half of the eighteenth century, as at the same time the first popular presentation and the starting point of modern behaviorism. It was known at that time as "natural history" and its outlines were rather vague, but Isidore Geoffroy St. Hilaire in 1859 clearly outlined its scope under the name of "ethology," and Haeckel in 1866 and 1869 even more accurately defined it as "Relations-Physiologie der Thiere," though he called it "oecology." In 1888 Carl Semper designated it as the "Physiologie der Organismen" to distinguish it from the "Physiologie der Organe," and in 1894 Burdon Sanderson published the following lucid statement:

"Now the first thing that strikes us in beginning to think about the activities of an organism is that they are naturally distinguishable into two kinds, according as we consider the action of the whole organism in its relation to the external world or to other organisms, or the action of the parts or organs in their relation to each other. The distinction to which we are thus led between the *internal* and *external* relation of plants and animals has of course always existed, but has only lately come into such prominence that it divides biologists more or less completely into two camps—on the one hand those who make it their aim to investigate the actions of the organism and its parts by the accepted methods of physics and chemistry, carrying the investigation as far as the conditions under which each process manifests itself will permit; on the other, those who interest themselves rather in considering the place which each organism occupies, and the part it plays in the economy of nature. It is apparent that the two lines of inquiry, although they equally relate to what the organism *does* rather than to what it *is*, and therefore both have equal right to be included in the one great science of life, or biology, yet lead in directions which are scarcely even parallel. So marked, indeed, is the distinction that Professor Haeckel some twenty years ago proposed to separate the study of organisms with reference to their place in nature under the designation of 'oecology,' defining it as comprising 'the relations of the animal to its organic as well as to its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes into direct contact.' Whether this term expresses it or not, the distinction is a fundamental one. Whether with the oecologist we regard the organism in relation to the world, or with the physiologist as a wonderful complex of vital energies, the two branches have this in common, that both studies fix their attention not on stuffed animals, butterflies in cases, or even microscopical sections of the animal or plant body—all of which relate to the framework of life—but on life itself."

E. Ray Lankester in 1889 also stressed the importance of ethology but called it

"bionomics," a term which has been little used. For many years the Germans have been employing "Biologie" *sensu stricto* for the same subject, while French zoologists, following the lead of Alfred Giard, retained St. Hilaire's designation. Emery and Waxweiler speak of it as "external physiology" and regard it as a preliminary or exploratory science destined eventually to be absorbed in physiology proper. That "behaviorism" is merely the most recent and most fashionable name for this long-established department of biology is sufficiently clear from the practical identity of Watson's and Burdon Sanderson's definitions. It may also be recalled, in connection with the first sentence of Watson's definition that John Stuart Mill in his Logic (1843) preceded St. Hilaire in the use of the term "ethology" for the science of human character, but since the character of an organism is revealed only in its reactions to its environment, that is by its behavior, there is no fundamental difference between animal and human ethology. Recently Bernard Hollander in his voluminous work "In Search of the Soul" calls attention to Mill's use of the term and adopts it for what is essentially human behavior.

It is evident, therefore, that there is nothing startlingly novel in the conceptions and methods employed by Watson and that both he and the psychologists seem to have been duped by a new word for an old thing. No doubt their deception is also due to the fact that the methods of ethological, or behavioristic science have proved to be so illuminating that, as Watson says (p. 17), "behavioristic formulations are becoming central in the whole field of what has hitherto been called 'the mental and moral sciences.'" In other words, ethological methods have been so rapidly and so aggressively invading philosophy, ethics, sociology and religion that serious doubts have arisen among modern thinkers as to the usefulness of the concepts and methods which have been so long employed in those domains. *Hinc illæ lacrymæ* on the part of the old doctinaires.

If the foregoing considerations are kept in mind it is not difficult to evaluate Watson's work. In so far as it is physiology of the type known to biologists as ethology, or relational physiology, it is of the greatest interest and value, not only to them but also to the humanists, if we use that term to include all students of the Hominidæ—anthropologists, psychologists, sociologists and ethicists. His statements, however, on specifically psychological matters cannot be taken seriously. The obvious fallacies involved in the behaviorist's rejection of the data obtained by introspection in the domain of immediate experience have been set forth by a number of authors, and most recently by E. D. Martin, Driesch and Broad. As Driesch clearly states, "Even if the behaviorists were right in saying that the only class of conscious objects are sensations" [Watson would seem not to accept even these] "this very statement would itself be the result of 'introspection'! And further to what class of objects belongs the *truth* of the behavioristic theory itself, that there is nothing but sensations? Is this specific truth itself a sensation? The behaviorists would hardly dare assert that it is, I fancy. So we may say, in short, that the behaviorist *forgets himself* in his psychological theory. Behaviorism is a good method,—nay, the only method—in animal psychology; indeed in this part of psychology, all knowledge that is really 'psychological' can be acquired only indirectly, never directly, for the movements of the body are the only things

that are given immediately. But in what we may call the *first*, the original psychology, i.e. *my* psychology, conditions are, fortunately, different. And it is for this reason that all other psychologies, the psychology of the *other Ego* of animals, of instincts, etc., must go back to the first psychology as their very foundation. Not to use introspection in 'my' psychology would be to proceed as if I always made use of a mirror in order to see what I might see directly—or even worse!" And Broad goes so far as to class behavioristic views like Watson's among the "silly" theories, by which he means those that "may be held at the time when one is talking or writing professionally, but which only an inmate of a lunatic asylum would think of carrying into daily life. I should count Behaviourism, taken quite strictly, and certain forms of Idealism as 'silly' in this sense. No one in his senses can in practice regard himself or his friends or enemies simply as ingenious machines produced by other machines, or can regard his armchair or his poker as being literally societies of spirits or thoughts in the mind of God. It must not be supposed that the men who maintain these theories and believe that they believe them are 'silly' people. Only very acute and learned men could have thought of anything so odd or defended anything so preposterous against the continual protests of common sense "

Those who have come to regard living organisms as at the same time creative and remarkably conservative, historical beings will notice that Watson is little affected by such considerations and inclined to overstress the effects of environment and to underestimate the complexity of organized and inherited structure. He seems to regard all healthy infants as very much alike at birth and to account for their later differences as very largely due to the conditioning, reconditioning and unconditioning of their reflexes, to visceral and muscular habits, training, etc. The geneticists are dismissed (p. 78) with an amusing fiction about three hypothetical sons of John Smith, the economist, and the remark, "the geneticists are working under the banner of the old 'faculty' psychology. One need not give very much weight to any of their present conclusions." Similarly the psychoanalysts, many of whom have stressed the persisting ancestral tendencies of our species, are said to base their work "largely upon religion, introspective psychology, and voodooism," and this notwithstanding the fact that Watson has absorbed many of their teachings. They are also presented (p. 244) with a fictitious and amusing account of a psychopathic dog. Watson describes how he conditioned a normal dog till he became a most abjectly insane animal and how he then unconditioned and reconditioned him till he walked off with the blue ribbon at the dog show. All this is humorous but hardly fair to the psychoanalysts or admissible as a popular account of their views. The importance of environment and training may be underestimated by many biologists of the present time, but there is certainly a much greater "historical basis of reaction" in animals and man than Watson would have us believe. Yet notwithstanding all its faults, the volume will be found to contain a great amount of valuable matter, especially on infant behavior, and many fresh incentives to the further investigation of man's basic nature.

BRIEF NOTICES

EVOLUTION

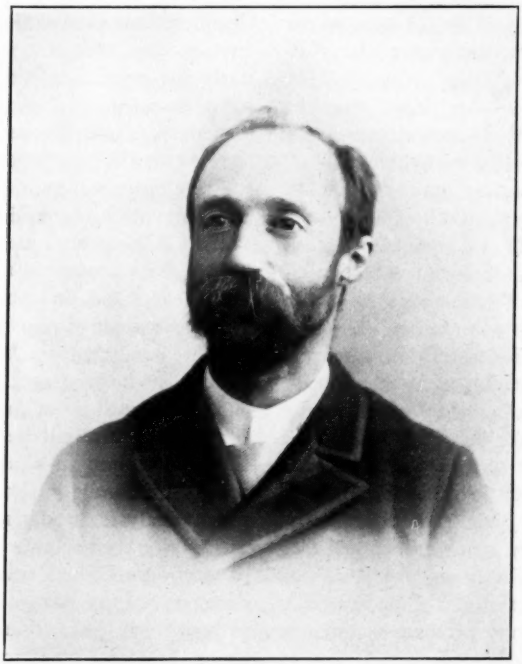
EVOLUTION EXAMINED IN THE LIGHT OF REVELATION AND REASON

By Albert P. Schack *Frederick H. Hitchcock* $2.50 $6\frac{1}{2}$ x $8\frac{3}{4}$; 121 *New York*

Physiognomy is not yet an exact science. Nevertheless, as Galton recognized when he began his work on composite photography, everyone is considerably influenced in his judgments regarding the practical conduct of life, by physiognomic considerations. Experience demonstrates that, on the whole, these judgments are far more often right than wrong.

We feel certain that few biologists personally know the more distinguished Fundamentalists. The parties to any controversy ought, at least, to know what their opponents look like. To this end we propose to publish in THE QUARTERLY REVIEW OF BIOLOGY, as opportunity and occasion may offer, a *Fundamentalist Portrait Gallery*.

It is with great satisfaction that we open this exhibition with the portrait of the eminent divine and author, Albert P. Schack.



ALBERT P. SCHACK

Evolution Examined in the Light of Revelation and Reason is a book that all biologists should read. Its provenience is set forth as follows by the author (p. 6): "A few years ago, the lack of a work, and the demand for one, by some author capable, by sufficient education and preparation, which should rightly un-

fold the subject, and make it plain to the people, and at the same time withstand the scrutiny and criticism of all the scientists, kept pressing upon me, so that I finally decided, having been thus suitably prepared by education, as well as by a careful study of the specific subject in all its aspects, that I might properly undertake the work for the sake of humanity, and for the honor of God and the Divine Truth."

Mr. Schack holds that "all kinds of life, or specific principles, are *inserted*, and are not evolved or developed merely out of and by the forms themselves," though he admits that this is often the appearance of things. "As an example or illustration of life entering and animating suitable forms, I have put a hair from a horse's tail in a vessel of water for some days, and have seen one end of it swell into a head, distinctly visible under a magnifying glass; and life flowing into it, which may be supposed to be everywhere imminent or outpressing from within, it became a snake or eel swimming in the water, because it was such a suitable sheath or form that such corresponding primitive life could inhabit and use it. This simple experiment can be tried by anyone, and the result will be seen to be as above stated" (p. 15).

The reviewer finds it difficult to refrain from quoting extensively from this informing volume, but considerations of space are imperative. We must content ourselves, therefore, with one more extract, which constitutes the whole of Chapter XI. It is not only interesting in content, but is also something of a literary feat. Few books can boast of a chapter which consists of only one sentence!

WARNING TO STUDENTS

"Hence I would warn those who are tempted to be seduced by the seemingly plausible hypotheses of the really blind materialists, to hold fast to the Word of God, not allowing the few portions of it which seem objectionable or difficult to understand, to prevent them from receiving it as a whole, or the vastly larger portion, which should not be objectionable to any, and of which we can get some understanding, if we study it, and humbly ask the Lord to help and enlighten us; recollecting that the whole Word is primarily and in some parts solely parabolic or symbolic of spiritual or internal things—motives—goodness and truth against evil and falsity, and in general of matters relating to God and the human soul" (pp. 102 and 103).

This book is priceless, in the technical Britannic sense of that word.

INDIAN BIRD LIFE. *Or the Struggle for Existence of Birds in India.*
By Douglas Dewar

John Lane, the Bodley Head
7s. 6d. $5\frac{1}{2} \times 7\frac{1}{2}$; xv + 276 *London*

This is an important, original contribution to the literature of organic evolution. It deals with the problem of checks to the avian population in India, on the basis of specific field observations rather than upon pseudo-philosophic platitudes, which all too frequently appear in lieu of evidence in the literature of evolution. Coupling extensive personal observations in the field with a remarkably thorough combing of the detailed ornithological literature, the author attempts to determine into which of the following categories the checks to avian population growth actually fall:

"1. Those of which the operation is entirely indiscriminate or haphazard; such operate equally on the fit and unfit, the weak and the strong, birds of gay plumage and birds of sombre hue.

"2. Those of which the operation is largely indiscriminate or haphazard.

"3. Those which operate only on the unfit, the weak, or birds ill-adapted to their environment.

"4. Those which operate mainly on the unfit, the weak, or birds ill-adapted to their environment" (p. 258).

The conclusions reached are as follows: "From the facts that the greatest destruction is to eggs and young birds and that the forces which destroy adult birds for the most part act indiscriminately as opposed to selectively, the inference must be drawn that, speaking generally, the individuals which survive longest in the struggle for existence are the lucky ones, rather than the most fit. It is, of course, true that other things being equal, the individuals which are fittest or strongest or best suited to their environment will have the best chance of survival. As a matter of fact other things are rarely equal. The existence of a bird may perhaps not inaptly be compared to a game of cards in which the element of chance is a very important factor. Although it is agreed that *A* is the most skilled of the players taking part in the game, no one, before any particular game, would give long odds on *A* winning, because far more depends on the hands dealt than on the skill of the players. So is it with birds. If we mark down, let us say, four individuals of a species, each living in an area at a distance from the others, it would not be prudent to give odds that the strongest of the four individuals will outlive the other three. The struggle for existence of birds results in the weeding out of the unlucky rather than the less fit.

"In view of the evidence before us it seems difficult to accept the view held by some that all the physical and anatomical features of every species are the result of a process whereby only the fit survive to produce young, which tend to inherit the fitness of the parents. Rather are those characteristics the result of the innate tendency of the majority of individuals of a species to vary in certain definite directions. Natural selection, the survival of the fittest, seems normally to come into action where variations markedly unfavourable to the individual appear.

"Natural selection, then, seems to have played only a very subordinate part in the production of the colouring and the anatomical and physical features of the various species of birds. This, however, does not mean that it has not played its part in evolution. There are conditions in which the force comes actively into play. Natural selection, for instance, has probably helped to determine such features as the number of eggs which compose the normal clutch for each species, the number of clutches laid in the year, the time of nesting, the situation of the nest, the times of migration and the degree of pugnacity possessed by the average individual of any species" (pp. 260–261).

The book is of interest and value to the student of the biological aspects of the population problem, as well as to the evolutionist. Unfortunately it is not adequately indexed, but after all this is only a minor defect in a really significant contribution.

LIFE, MIND, AND SPIRIT. (*Being the Second Course of The Gifford Lectures Delivered in the University of St. Andrews in the Year 1923 under the General Title of Emergent Evolution.*)
By C. Lloyd Morgan *Henry Holt and Co.*
$3.75 $5\frac{7}{8}$ x 9; xix + 316 *New York*

This book attempts to formulate a

philosophical interpretation of the order of nature—the evident teleological structure and behavior of the universe. The solution offered is frankly theistic. Essentially the order of nature is Divine Purpose objectively expressed, and there the case rests. This manner of disposing of the problem is neither particularly novel, nor, as the whole history of philosophic thought shows, especially helpful. At the same time it must be said that the author puts the case in an extremely persuasive way, much better calculated to seduce the modern scientific reader than, for example, were the writings on natural theology of the eighteenth and early nineteenth centuries. Biologists will do well to read this book.

THE RELATION BETWEEN SCIENCE AND THEOLOGY. (*How to Think About It.*)

By C. Stuart Gager

The Open Court Publishing Co.

$1.00 5 x 8; 87 *Chicago*

This little tract of the times is written in a spirit of deep reverence—both to God and to science. Its philosophy is summed up in the following statement: "What has evolution to do with religion? In a sense, nothing. Science has to do with so-called secondary causes; religion has to do with man's relation to the Great First Cause—Myself and God" (p. 79). As a bit of conciliatory exegesis it is well done.

THE PASSING OF THE PHANTOMS. *A Study of Evolutionary Psychology and Morals.*

By C. J. Patten

Kegan Paul, Trench, Trubner and Co.

2s. 6d. 4½ x 6½; 95 *London*

The author seems to be more sympathetic than coldly analytic in his experiences with family pets, especially a hawk. He attributes a somewhat higher psychic life to lower animals than perhaps most students of animal behavior are disposed to do. On this not wholly indubitable base he builds up a theory of the evolution of man's mental and moral powers. The book is more entertaining than convincing.

THE STRATIGRAPHY AND FAUNA OF THE HACKBERRY STAGE OF THE UPPER DEVONIAN. (*Contributions from the Museum of Geology, University of Michigan. I.*)

By Carroll L. Fenton and Mildred A. Fenton

The Macmillan Co.

$2.75 6¼ x 9¼; xi + 260 *New York*

Describes, with abundant illustrations on 45 plates, the fossils found in the uppermost member of the Devonian section (the rocks of the Hackberry stage) in North Central Iowa.

GENETICS

HEREDITY

By A. Franklin Shull McGraw-Hill Book Co.

$3.00 6¼ x 9¼; xi + 287 *New York*

An excellent introductory text to the field of modern genetics. Developed in connection with a lecture course to large classes of college students without preliminary biological training, the book has solved well the difficult pedagogical problem of presenting an intricate subject in a clear, attractive, and at the same time thoroughly sound, manner. Those giving beginning courses in genetics in colleges and universities will do well to consider it carefully for use as a text. Furthermore it is, on the whole, the best book that has come to our attention for the intelligent layman who wishes to get

a sound understanding of the fundamental principles of heredity. The last eight chapters are devoted to various aspects of human genetics. A glossary of technical terms and an adequate index complete the volume.

PRAKTISCHE ÜBUNGEN ZUR VERERBUNGSLEHRE FÜR STUDIERENDE, ÄRZTE UND LEHRER. *(In Anlehnung an den Lehrplan des Erbkundlichen Seminars von Prof. Dr. Heinrich Poll). (Biologische Studienbücher. Band I.)*

By Dr. Günther Just *Theodor Fisher*
Rm. 3.50 *Freiburg im Breisgau*
6½ x 9½; 88 (paper)

This is an outline of a course of eighteen laboratory exercises in genetics as used by the author and Professor Poll in an elementary course at Berlin. The first six exercises deal with the biometric analysis of variation; the next seven with the analysis of Mendelian experiments; and the last five with human pedigrees. It is a well planned elementary course.

THE THEORY OF THE GENE.
By Thomas Hunt Morgan
Yale University Press.
$4.00 6½ x 9¼; xvi + 343 *New Haven*

This book will be the subject of an extended review by Professor Julian Huxley, in the next number of THE QUARTERLY REVIEW OF BIOLOGY.

GENERAL BIOLOGY

NATURALIST'S GUIDE TO THE AMERICAS. *Prepared by the Committee on the Preservation of Natural Conditions of The Ecological Society of America, with assistance from numerous organizations and individuals. Assembled and edited by the Chairman, Victor E. Shelford.*

The Williams & Wilkins Co.
$10.00 6¼ x 9¼; xv + 761 *Baltimore*

This comprehensive treatise, produced by the coöperative efforts of The Ecological Society of America, discusses in detail the natural habitat for living things in North America, Central America, and the northern part of South America, together with certain of the islands in the Atlantic and Pacific Oceans. The first three parts of the book are devoted to the uses, values, and management of natural areas and the original biota of the Americas north of the Amazon. The fourth part, which takes up the bulk of the book, is devoted to detailed descriptions of natural areas and regions within named political subdivisions. The primary object of the book is stated to be "To locate natural areas so as to make them available to naturalists." For each territory the account describes: (1) the region as it was before being modified by civilization; (2) the general physiographic features, and (3) general and local plant and animal communities. The original conditions of the biota are then contrasted with the present modified condition. The book is a valuable contribution to the literature of general natural history.

ERGEBNISSE DER BIOLOGIE.
Edited by K. v. Frisch, R. Goldschmidt, W. Ruhland and H. Winterstein.

Julius Springer
36 reichsmark *Berlin*
6½ x 9½; viii + 670 (paper)

The QUARTERLY REVIEW OF BIOLOGY extends a hearty welcome to this new periodical which in some sense covers the same field. It is announced that the *Ergebnisse der Biologie* will treat general

physiology (as distinguished from physiology primarily of medical interest) in much the same way that the *Ergebnisse der Anatomie und Entwicklungsgeschichte* and the *Ergebnisse der Physiologie* deal with their respective fields. This first number opens with a paper of 323 pages by E. Biedermann on the comparative physiology of the integument of vertebrates. The second paper is by F. Bachmann on the ascent of sap in plants. The third is by Hugo Kaho on the relation of the plant cell to salts. The fourth paper, by D. N. Prianischnikow, deals with ammonia, nitrates and nitrites as nitrogen sources for higher plants. The two final papers discuss respectively the social psychology of birds (by David Katz), and bird migration (by Horst Wachs). There are detailed indices and literature lists.

LA CINÉTIQUE DU DÉVELOPPEMENT. *Multiplication cellulaire et Croissance.*

By E. Fauré-Fremiet (Preface by M. L. F. Henneguy)

Les Presses Universitaires de France

30 francs $6\frac{1}{2}$ x $9\frac{1}{2}$; viii + 335 *Paris*

This is an important and valuable addition to the literature of general biology. It reviews the existing knowledge and opinion about the physics and chemistry of growth and development in a thorough manner. The material is discussed under the following heads: The cellular system from a static point of view; cellular growth; the changes of state in the cellular system in the course of division; the transformations of energy in the course of embryonic development; the laws of growth of the body and of the organs; the multiplication of free cells—Protozoa; the multiplication of cells *in vitro*—tissue cultures. There are extensive bibliographies, but unfortunately an index is lacking.

COMPARATIVE PHYSIOLOGY

By Lancelot T. Hogben The Macmillan Co.

$3.00 $5\frac{3}{4}$ x $8\frac{3}{4}$; xiv + 219 *New York*

This book aims to give in brief space an account of the physiology of the lower organisms, primarily for the purpose of stimulating students of zoölogy to further research in this field. It is thoroughly modern in its viewpoint, emphasizing the physico-chemical approach to the problems of physiology. The topics treated are as follows: muscular contraction; ciliary activity, amoeboid motion and color response; secretion; respiration; nutrition; the circulation of body fluids; endocrine co-ordination; the mechanism of nervous conduction and excitation; the analysis of behavior in animals; the fertilization of the egg; inheritance; physiology of development.

PAPERS FROM THE DEPARTMENT OF MARINE BIOLOGY OF THE CARNEGIE INSTITUTION OF WASHINGTON. *Vol. XXIII (Publication No. 344). Some Marine Bottom Samples from Pago Pago Harbor, Samoa, by M. N. Bramlette. Proportions of Detrital Organic Calcareous Constituents and their Chemical Alteration in a Reef Sand from the Bahamas, by Marcus I. Goldman. Report on a Bacteriological Examination of "Chalky Mud" and Sea-Water from the Bahama Banks, by N. R. Smith. Recent Foraminifera from Porto Rico, by J. A. Cushman. Fossils from Quarries near Suva, Viti Levu, Fiji Islands, and from Vavao, Tonga Islands, with Annotated Bibliography of the Geology of the Fiji Islands, by Wendell C. Mansfield. Miocene Corals from Trinidad, by T. W. Vaughan and J. E. Hoffmeister.*

Carnegie Institution of Washington

$2.50 *Washington, D. C.*

$6\frac{7}{8}$ x 10; 134 + 7 plates (paper).

The contents of this volume seem

likely to be of greater interest to the oceanographer and the paleontologist than to the general biologist.

PRACTICAL PHOTO-MICROGRAPHY. *By J. E. Barnard and Frank V. Welch* *Longmans, Green and Co.* $6.00 5¾ x 8½; xii + 316 *New York*

A second edition, issued after a lapse of fourteen years since the appearance of the first, of the standard work in English on photo-micrography. The senior author, who has lately been much in the public eye in connection with his collaboration with Gye on the cancer problem at the Medical Research Council's laboratory in London, is one of the foremost authorities in the field. In the second edition attention has been primarily given to a fuller description of methods rather than apparatus, because the authors find no outstanding advance, either on the optical or mechanical side, in the past fourteen years. The book constitutes a standard reference source for all those who use photo-micrography in their work.

HUMAN BIOLOGY

THE NORTHERN TRIBES OF NIGERIA. (*An Ethnographical Account of the Northern Provinces of Nigeria Together with a Report on the 1921 Decennial Census.*) *By C. K. Meek* *Oxford University Press* 36s. 6 x 9; Vol. I, xviii + 312 *London* Vol. II, viii + 277

This work is an important contribution to anthropology. The material is logically arranged, presented with great clearness and some degree of literary charm, and considers data of interest and value to the student of almost any aspect of human biology. There is first given a general description of the country itself, considered as a habitat for human beings. This is followed by an historical section, with a good deal of interesting archaeological material. Then the various aspects of the native culture are considered in detail, beginning with the economic life. The political aspect of the cultural life is first discussed in relation to social organization, and then in regard to the system of government and law. The mental and spiritual life as revealed in language, law, and religion, receives thorough treatment. Part II of the second volume is of especial interest to students of the population problem, since it deals in detail with the census of the provinces of Northern Nigeria taken in 1921.

AUSTRALIAN TOTEMISM. (*A Psychoanalytic Study in Anthropology.*) *Géza Róheim (with an introduction by M. D. Eder)* *George Allen and Unwin, Ltd.* 35s. 6½ x 10; 487 *London*

Doctor Róheim attempts to explain the origin of the most primitive form of culture, totemism, on the theory that it is the result of a primeval crime, in which the sons of a Cyclopean family killed their tyrannical father, ate his body, and then married the females left about. Ever since then the sons, and their descendants, have been torn between the two emotions of repentant remorse over killing the old man, and triumphant joy at having got the ladies. As a result of these mixed emotions the taboos of incest and of eating the animal have grown up, as well as the ritual of totemic sacrament and organization into totem clans. It seems doubtful that this queer theory, reached by the psychoanalytic route, will be accepted by anthropologists. However, the author is a man of standing and marshals a large array of evidence with great ingenuity. On these accounts

the book cannot be lightly swept aside. It will interest the psychologist as well as the anthropologist. There is an extensive bibliography and index.

THE PEDIGREE OF THE HUMAN RACE.

By Harris H. Wilder *Henry Holt and Co.*
$3.25 6 x 9; xiv + 368 *New York*

A sound treatise on the natural history of the primates has long been needed. This need is admirably met in the present book. One reads it with a feeling of confidence and security, because of the author's critical judgment in zoological matters. The book is divided into six chapters, of which the first reviews existing knowledge regarding the groups of primates now living. Chapter II deals with extinct forms related to man, reviewing the history of mammalian evolution. Chapter III treats of fossil men. Chapter IV, besides tracing the pedigree discusses the nature of the evidence and modes of reasoning by which present conclusions as to the evolution of man have been reached. Chapter V describes the differential characteristics of living races of men. The final chapter discusses the classification of human races. The book is well illustrated and indexed.

INTERNATIONAL ASPECTS OF BIRTH CONTROL. (*The Sixth International Neo-Malthusian and Birth Control Conference, Vol. I.*)
PROBLEMS OF OVERPOPULATION. *Vol. II.*
Edited by Margaret Sanger
American Birth Control League, Inc.
$2.00 5½ x 8½; xii + 244 (paper) *New York*
$2.00 5½ x 8½; 208 (paper)

These two volumes contain the official report of the proceedings of the International Birth Control Conference held in New York in March, 1925. The first volume is devoted to reports on the present status of the birth control movement in different countries and states of this country, together with congratulatory and uplifting messages from various prominent persons. The second volume is devoted to the more scientific papers which were read. Students of the population problem may find these volumes useful for reference, although they contain little that is original. Unfortunately there is no index.

THE MEDICAL DEPARTMENT OF THE UNITED STATES ARMY IN THE WORLD WAR. VOLUME XV. STATISTICS. *Part 2. Medical and Casualty Statistics (Based on the Medical Records of the United States Army April 1, 1917, to December 31, 1919, inclusive).*
By Maj. Albert G. Love
Government Printing Office
$3.00 *Washington, D. C.*
7¾ x 10; xiv + 1368

A potentially profitable source book for the student of human biology.

ZOOLOGY

THE BIOLOGY OF THE PROTOZOA. *By Gary N. Calkins* *Lea and Febiger*
$7.50 6¼ x 9½; ix + 623 *Philadelphia*

This is a masterpiece of textbook writing and is certain to become a classic in the field which it so thoroughly covers. The plan and scope of the book are sufficiently indicated by the chapter headings which are as follows: Introduction; Nuclei and kinetic elements; Structural differentiations; General physiology; Reproduc-

tion; Special morphology and taxonomy of the Mastigophora; Special morphology and taxonomy of the Sarcodina; Special morphology and taxonomy of the Infusoria; Special morphology and taxonomy of the Sporozoa; Vitality; Phenomena accompanying fertilization; Effects of reorganization and the origin of variations in the Protozoa. An enormous amount of careful painstaking, critical work must have gone into the preparation of the taxonomic portions of the treatise, and they will be correspondingly useful to all students of protozoology. Throughout the book the author stoutly maintains his well known position regarding the theoretical significance of the life cycle of Protozoa, a position with which many other biologists are not in entire agreement.

BIOLOGIE DER SCHMETTERLINGE. (*Biologische Studienbücher. III.*)
By Dr. Martin Hering *Julius Springer*
Rm. 18 6½ x 9½; vi + 480 (paper) *Berlin*

The introduction to this detailed treatise on the biology of butterflies deals first with their general anatomy, then with their phylogeny and taxonomic relationships. This introductory portion is followed by three main sections which take up the bulk of the book. The first of these deals with the ontogenetic development up to the imago; the second with the life of the imago; and the third with general problems, such as geographic distribution, alternation of generations, polymorphism, enemies of butterflies, experimental biology, etc. There is a brief bibliography of general works, and adequate indices. Altogether this is a welcome addition to zoological literature, in a direction to which textbook writing seems to be definitely turning—the preparation of more adequate treatises on special groups than can possibly be included in general textbooks.

A WILD-ANIMAL ROUND-UP. (*Stories and Pictures from the Passing Show.*)
By William T. Hornaday
Charles Scribner's Sons
$5.00 6½ x 9; xii + 372 *New York*

This contribution to the literature of popular natural history by the Director of the New York Zoological Gardens is largely made up of previously printed magazine articles, going back in some cases to 1908. It falls into three main parts, the first dealing chiefly with big game hunting adventures, mostly in the early days in our own western country. Part II discusses mainly the disappearance of big game animals in various parts of the world. The final portion of the book is devoted to the modern development of taxidermy. Every lover of nature will find it an entertaining volume, though its science is perhaps sometimes a little rough and ready, and its manner occasionally transgresses the canons of good taste. It is well indexed and most interestingly illustrated.

THE NEMATODE PARASITES OF VERTEBRATES.
By Warrington Yorke and P. A. Maplestone, with Foreword by C. W. Stiles
P. Blakiston's Son and Co.
$9.00 6¼ x 10; xi + 536 *Philadelphia*

This is a thorough and detailed treatise on the taxonomy of the nematode worms living parasitically in vertebrate animals. It is extensively illustrated with line drawings, and contains adequate keys for the identification of the genera and a bibliography of 684 titles. In the Foreword there is an open letter ad-

dressed to "unborn helminthologists." It makes an impassioned and touching appeal that they do their taxonomic duty by worms, when their time comes. This letter adds just that serious touch needed to avert whatever slight possibility there might otherwise have been that this book as a whole would be taken in a spirit of levity. For who could contemplate the idea of an "unborn helminthologist" lightly?

ZOOLOGIE IM GRUNDRISS.
By Walter Stempell *Gebrüder Borntraeger*
6,90 marks *Berlin*
Lieferung 3, 7⅛ x 10½; 178 (paper)
6,60
Lieferung 4, 7⅛ x 10½; 176 (paper)

The third *Lieferung* of this general textbook of zoology already noticed in Number 2 of THE QUARTERLY REVIEW completes the first section dealing with morphology and taxonomy, and makes a beginning on the second main division of the work, which treats of physiology and development. This physiological section starts with a discussion of the composition of the body, followed by an account of the metabolism of material. This is followed, in the fourth instalment, by a discussion of the metabolism of energy, which includes a long section on the reactions of animals to stimuli. The account of reproduction and embryonic development is begun.

A NATURALIST IN EAST AFRICA.
Being notes made in Uganda, ex-German and Portugese East Africa.
By G. D. Hale Carpenter.
Oxford University Press
15 shillings 6 x 9; 187 + 8 plates *London*

Dr. Hale Carpenter, well known for his interesting book of a few years ago, "A Naturalist on Lake Victoria," again publishes a series of extracts from his notebooks of observations collected during his wanderings as an officer of the Uganda Medical Service. The result is a valuable contribution to natural history, especially in regard to the problems of variation and mimicry in butterflies. Perhaps the most important part of the book is a detailed account of extensive experiments on the relative edibility of insects. It is well illustrated and indexed.

ANIMAL LIFE IN THE SEA.
By R. J. Daniel *Hodder and Stoughton, Ltd.*
5s. 6d. 5¾ x 8¾; 119 *London*

This little book, written in a simple and lucid style, evidently intended for lay readers, is a fine example of popular science at its best. The contents are as follows: Life in the shallow seas; The deep sea; Some large fish of the sea; The giant squid; Some whales; Some extinct marine monsters; The great sea serpent. It is entertainingly and significantly illustrated. We commend it to our readers, and congratulate the author on so fine an achievement.

THE SECRETS OF THE EAGLE AND OF OTHER RARE BIRDS.
By H. A. Gilbert and Arthur Brook
Arrowsmith
10 shillings 6¾ x 8¾; 196 *London*

The superb photographs of birds reproduced in this volume make it worthy the serious attention of zoologists. Nearly half the book is devoted to the golden eagle, its nest and nestlings. Some of the other birds discussed and photographed are not particularly rare, but the

photographs of them are highly unusual in quality. Every student of birds, whether professional or amateur, will find delight in this book.

L'ÉVOLUTION DE L'ORNITHOLOGIE. *By Maurice Boubier* *Félix Alcan*
10 francs $4\frac{3}{4}$ x $7\frac{1}{2}$; 308 (paper) *Paris*

There is a real need for brief but comprehensive and accurate histories of the various sub-divisions of the biological sciences. An excellent contribution in this direction for ornithology is made by Doctor Boubier in this volume. It recounts in a pleasant and easy style the development of knowledge about the various aspects of ornithology. It should be in every general biological library.

TAXIDERMY AND MUSEUM EXHIBITION. *By John Rowley. (Preface by Frank M. Chapman.)* *D. Appleton and Co.*
$7.50 $6\frac{1}{4}$ x $9\frac{1}{2}$; xvi + 331 *New York*

In this comprehensive didactic treatise America's foremost taxidermist details the secrets of his craft. As in any other art, it is probable that in taxidermy genius cannot be transferred by teaching, but so far as technical equipment is concerned, this book covers the ground thoroughly. It will be the standard work on the subject for a long time to come. It is fully illustrated and indexed.

PORTRAITS IN THE LONDON ZOO. *By Silvia Baker* *G. P. Putnam's Sons*
15 shillings $7\frac{3}{4}$ x $10\frac{1}{4}$; 111 *London*

This delightful book will charm every lover of animals. The text is insignificant in amount and unimportant in content, but the tinted line drawings are superb. With an economy of line which suggests Rouveyre, the artist has imbued her figures of all sorts of animals with real life and character.

A KEY TO THE SNAKES OF THE UNITED STATES, CANADA, AND LOWER CALIFORNIA. *(Michigan Academy of Science, Arts and Letters. Vol. IV. Part II.)*
By Frank N. Blanchard *The Macmillan Co.*
$1.75 $6\frac{1}{4}$ x $9\frac{1}{2}$; xiii + 65 *New York*

This useful key lists 191 species and subspecies of North American snakes, exclusive of continental Mexico and Central America. The characters used for identification do not involve any necessity for dissection or for examination of teeth. Data are given on the geographic distribution of each species and subspecies.

PAPERS FROM THE DEPARTMENT OF MARINE BIOLOGY OF THE CARNEGIE INSTITUTION OF WASHINGTON. *Vol. XXIV (Publication No. 345). Taxonomy of the Amebas with Descriptions of Thirty-nine New Marine and Freshwater Species.*
By Asa Arthur Schaeffer
Carnegie Institution of Washington
$4.75 *Washington, D. C.*
$9\frac{1}{4}$ x $11\frac{1}{2}$; 116 + 12 plates (paper)

In this beautifully illustrated monograph the author describes 39 new species and 11 new genera of amebas, and proposes a system of classification for the group based upon general morphology. In connection with the descriptions of the species numerous interesting observations on behavior and physiology are included.

REPORT ON A COLLECTION OF SEA TROUT SCALES FROM THE RIVER HOPE AND LOCH HOPE IN SUTHERLAND. (*Fishery Board for Scotland. Salmon Fisheries. No. 1.*)
By G. Herbert Nall *H. M. Stationery Office*
3 shillings $6\frac{1}{8}$ x $9\frac{3}{4}$; 22 (paper) *Edinburgh*

Original data of interest to anyone working on the problems of growth or senescence.

BOTANY

THE SCENT OF FLOWERS AND LEAVES. *Its Purpose and Relation to Man.*
By F. A. Hampton *Dulau and Co., Ltd.*
6 shillings $5\frac{1}{8}$ x $7\frac{1}{2}$; vii + 135 *London*

This is an extremely interesting and entertaining little book about a neglected aspect of botany. It is simply and pleasantly written, but contains a wealth of unusual information. The topics treated are as follows: The sense of smell; Composition of the scent; Origin and development of the scent; Distribution of the essential oil in the plant; Function of scent; Insects and the scent of flowers; Scent in relation with botanical character; Classification; Our appreciation of scent; Scent in the garden; Extraction of scent and the manufacture of perfume; History. The book is adequately indexed.

THE FAMILIES OF FLOWERING PLANTS. I. DICOTYLEDONS. *Arranged According to a New System Based on Their Probable Phylogeny.*
By J. Hutchinson *Macmillan and Co.*
$6.00 6 x 9; xiv + 328 *London*

The principles on which this new systematic arrangement of the families of flowering plants are based are these: Plants with sepals and petals, associated with other floral and anatomical characters also primitive, are regarded as more ancient phylogenetically than plants without sepals or petals. This is based on the theory that the parts of an angiospermous flower are modified leaves. Free parts are regarded as primitive, and connate or adnate parts as more recent. The spiral arrangement of parts is regarded as more primitive than the cyclic, and numerous free stamens as earlier than the few or connate. Also the hermaphrodite flower is regarded as preceding the unisexual flower. Resemblances are emphasized rather than differences. The book is well illustrated and indexed.

PHYSIOLOGICAL FEATURES OF ROOTS, WITH ESPECIAL REFERENCE TO THE RELATION OF ROOTS TO AERATION OF THE SOIL. (*With a Chapter on Differences Between Nitrogen and Helium as Inert Gases in Anaerobic Experiments on Plants, By Edward E. Free.*)
By William Austin Cannon
Carnegie Institution of Washington
$1.25 *Washington, D. C.*
7 x 10; iii + 168 (paper)

With great elaboration of detail this book reports the results of a critical experimental study of the relation of root growth to soil aeration in a wide range of plants. The two main topics dealt with in the research are: First, the effect on root growth of concentrations of carbon dioxide in the soil; and, second, the influence of oxygen supply. An interesting point of general biological significance is the emphasis laid upon the individuality of the plant as a factor in the physiological results obtained. This factor is too often neglected by both plant and animal physiologists.

BIOLOGIE DER BLÜTENPFLANZEN. *(Eine Einführung an der Handmikroskopischer Übungen.) (Biologische Studienbücher. Band II.)*

By Prof. Dr. Walther Schoenichen *Theodor Fisher*

Rm. 6.60 *Freiburg im Breisgau*

6½ x 9½; 216 (paper)

The topics dealt with in this brief practical introduction to plant biology are: The biology of the root; the biology of the stem; the biology of leaves; the biology of the flower; the distribution of seeds and roots. It is fully and significantly illustrated with 307 line cuts, all semidiagrammatic in character, but in the clearest possible way bringing out the principles which they are intended to illustrate. It should be translated into English.

PLANT DISEASE FUNGI.

By F. L. Stevens *The Macmillan Co.*

$5.00 5¾ x 8¾; vi + 469 *New York*

This is a thorough, systematic treatise on the taxonomy and morphology of fungi pathogenic to plants. The book is well illustrated and has determinative keys to the genera. Descriptions of diseased hosts are omitted.

MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Vol. XVII, Nos. 85 to 89. (Publication No. 362.) No. 85. Development of the Human Embryo During the Period of Somite Formation, Including Embryos with 2 to 16 Pairs of Somites, by George W. Bartelmez and H. M. Evans. No. 86. Origin and Development of the Rete Ovarii and the Rete Testis in the Human Embryo, by Karl M. Wilson. No. 87. Physiological Study of Cortical Motor Areas in Young Kittens and in Adult Cats, by Lewis W. Weed and Orthello R. Langworthy. No. 88. Lymphatics and Blood-Vessels of the Ovary of the Sow, by Dorothy H. Andersen. No. 89. Relation of Onset of Decerebrate Rigidity to the Time of Myelinization of Tracts in the Brain-Stem and Spinal Cord of Young Animals, by Orthello R. Langworthy.*

Carnegie Institution of Washington

$3.25 *Washington, D. C.*

9¼ x 11½; 3 + 140 (paper)

This volume of contributions from the Carnegie Laboratory of Embryology well maintains the high standard which the biological public has learned to expect from this laboratory. The first paper in the volume is perhaps the one of greatest technical importance, while the last probably has the greatest general biological interest. It indicates a definite correlation between the time of myelinization of the central nervous system and the appearance of decerebrate rigidity.

L'ANATOMIE EN POCHE.

By Victor Pauchet and S. Dupret

Gaston Doin et Cie

25 francs 4½ x 7; 316 (paper) *Paris*

Each page of this little pocket anatomy contains a clear, somewhat schematic diagram of the structure of a small portion of the human body. Every feature shown on the diagram is then carefully labeled. The result is excellent. Almost at a glance the memory on a detailed anatomical point can be refreshed or reestablished. There are in all 297 of the little plates, and together they cover all the essential features of gross human anatomy. The book ought to be a boon to medical students, and to beginning surgeons.

THE HISTOLOGY OF THE MORE IMPORTANT HUMAN ENDOCRINE ORGANS AT VARIOUS AGES.
By Eugenia R. A. Cooper
Oxford University Press
$4.00 xiii + 119 *New York*

This is a useful piece of morphological work for investigators dealing with any phase of the endocrine problem. Detailed accounts are given of the normal histology, and the changes with age, of the pituitary, the suprarenal, the thyroid, the parathyroid and the thymus glands. It is well illustrated, chiefly with microphotographs. There is a bibliography of 112 titles, and detailed author and subject indices.

DIE PATHOLOGISCH-HISTOLOGISCHEN UNTERSUCHUNGSMETHODEN.
By Prof. Dr. G. Schmorl. F. C. W. Vogel
20 marks $6\frac{1}{4}$ x $9\frac{1}{2}$; x + 481 (paper) *Leipzig*

The fourteenth edition of this standard *vade-mecum* of histological methods in the field of pathology, differs chiefly from the last preceding edition in the fact that the chapters on embedding and frozen section technique have been rewritten. Zoological laboratories will find this a useful reference work.

ELEMENTS OF SURFACE ANATOMY. (*For Students of Medicine.*)
By I. Maclaren Thompson
E. and S. Livingstone
5s. $5\frac{1}{4}$ x $7\frac{1}{2}$; 172 *Edinburgh*

This little guide for the location on the surface of the body of deeper lying anatomical structures will probably be found most useful by medical students in connection with their training in physical diagnosis. The entire omission of illustrations is a defect. There is a detailed index.

STUDIES ON THE MORPHOLOGY AND MORPHOGENESIS OF HUMAN THORACOPAGIC MONSTERS. *With Special Reference to the Malformation of the Heart.*
By Fredrik Ysander Almqvist and Wiksells
Swedish Kr. 5 *Uppsala, Sweden*
6 x 9; viii + 236; 11 plates (paper)

This inaugural dissertation contains a detailed description of eight specimens of early human thoracopagic monsters; a summary of the reports of such double monsters in the literature between 1911 and 1922; and a discussion of the morphology and morphogenesis of these monsters. It is illustrated with 11 photogravure plates.

PHYSIOLOGY

HELMHOLTZ'S TREATISE ON PHYSIOLOGICAL OPTICS. (*Translated from the Third German Edition*) *Vols. I, II and III.*
By H. von Helmholtz. (Edited by James P. C. Southall.) The Optical Society of America
$7 per volume; *Ithaca, N. Y.*
$21 per set.
$7\frac{1}{2}$ x $10\frac{3}{4}$; Vol. I, xxi + 482
Vol. II, viii + 480
Vol. III, x + 736
(Orders should be sent to F. K. Richtmyer, Secretary of The Optical Society of America, Rockefeller Hall, Ithaca, N. Y.)

The Optical Society of America has done a useful service to physiology by making available for the first time a complete translation in English of Helmholtz's great classic on physiological optics. The translation is from the third and definitive German edition which originally appeared in the years 1909 to 1911. In three large and stately volumes,

well printed and well bound, it should find a place on the shelves of every physiological laboratory. The translators have wisely adhered to the German text in the form in which it was left in the third edition, attempting to bring the material up to date only in the following ways: First, by the addition of a chapter on ophthalmoscopy, by Gullstrand; second, by the addition of several special contributions by von Kries; third, by the insertion of an article by Christine Ladd-Franklin on her theory of color; and, finally, by the addition throughout the entire work of some references to recent literature. In the main, however, the bibliographic references are left about as they were in the third German edition.

The distribution of the material in the three volumes is as follows: Volume I contains, first, an anatomical description of the eye, followed by Part I of the physiological optics, dealing with the dioptrics of the eye. Volume II discusses the sensations of vision, and Volume III the perceptions of vision.

Indices covering 29 pages complete the work. The translation and editing of this monumental work appear to have been done with great critical care and excellent judgment.

HUMAN METABOLISM WITH ENEMATA OF ALCOHOL, DEXTROSE, AND LEVULOSE. (*Publication No. 369.*)
By Thorne M. Carpenter
Carnegie Institution of Washington
$2.25 6¾ x 10; ix + 197 (paper) *Washington, D. C.*

This extremely detailed account of a long experimental research shows that alcohol injected rectally is retained by the body and enters into its tissues, the absorption being over 98 per cent. Studies of the alcohol in urine in short periods indicate that the utilization of alcohol is practically complete at the end of five hours, and is very high in the first one and one-half hours. The proportion of the total metabolism due to alcohol injected may be as high as 51 per cent. The utilization of alcohol in rectal feeding plays a prominent rôle in the total metabolism.

RECENT ADVANCES IN PHYSIOLOGY.
By C. Lovatt Evans
P. Blakiston's Son and Co.
$3.50 5½ x 8¼; xi + 364 *Philadelphia*

We cannot too highly recommend this book to our readers. In the words of its author "Its aim is to present to the student who has worked through an ordinary text-book an account of some of the problems with which physiologists have been concerned during recent years, and thus to serve, not only to enrich the student's knowledge as regards subjects of contemporary interest, but also to form a convenient bridge by which he may, if he feels so disposed, pass more easily into the original literature of those subjects." This highly intelligent and useful purpose has been extremely well accomplished by Dr. Lovatt Evans. The intriguing nature of the contents is apparent from their mere enumeration: Blood; Corpuscles and plasma; Suspension stability of blood; Origin of the blood cells, and their relation to the connective tissues; Fate of the red corpuscles; Carriage of carbon dioxide by the blood; Reaction of the blood; Output and work of the heart; Capillary circulation; Mechanism of tissue oxidations; Chemistry of muscular contraction;

Physical aspects of the physiology of muscular contraction; Application to the physiology of muscular exercise in man of the results of researches on the chemistry and physics of contraction; Active principles of some endocrine organs: thyroxin, pituitary principles, insulin; Mechanism of postural reflexes and the function of the labyrinth; Conditioned reflexes.

Adequate bibliographies of recent work follow each chapter. It is difficult to pick out for special mention any particular chapter of a book of such uniform excellence, but the final one on Conditioned Reflexes seems to us a masterpiece of clear and interesting scientific exposition.

LECTURES ON NUTRITION. (*A Series of Lectures Given at the Mayo Foundation and the Universities of Wisconsin, Minnesota, Nebraska, Iowa, and Washington (St. Louis).*

W. B. Saunders Co.

$2.50 5½ x 8; 243 pp. *Philadelphia*

This series of semi-popular lectures by distinguished authorities in the field of nutrition deals with the following subjects: The measurement and significance of basal metabolism, by Francis G. Benedict; Problems of metabolism, by Graham Lusk; The proportions in which protein, fat, and carbohydrate are metabolized in disease, by Eugene F. DuBois; Muscular activity and carbohydrate metabolism, by Archibald V. Hill; Our present knowledge of the vitamins, by Elmer V. McCollum; The Relations between fertility and nutrition, by Herbert L. Evans. Fairly extensive literature lists follow each chapter. The book will be useful for collateral reading in courses in general biology and physiology. Also the lay reader will find it a satisfactory means of getting in brief space a wide ranging view of the present state of knowledge regarding nutrition.

A COLLEGE TEXT-BOOK OF PHYSIOLOGY.

By Arthur D. Bush *Lea and Febiger*

$3.50 5¾ x 8; xiii + 331 *Philadelphia*

This new textbook of human physiology is designed to fill the gap in the textbook literature of this field which has existed by reason of the lack of any book especially adapted for college rather than for high school or for medical students. It covers the ground well, and seems admirably suited to the purpose. There are brief but well chosen reading lists following each of the twenty-two chapters. The book closes with a short glossary and index.

BASAL METABOLISM. *Determination of the Metabolic Rate in the Practice of Medicine. By John T. King, Jr.*

The Williams & Wilkins Co.

$2.50 6 x 9; 118 *Baltimore*

This is a brief review of the literature on basal metabolism, with special reference to the importance of such a study in the practice of medicine. There is a bibliography covering some 15 pages, and the book is well illustrated and indexed. It seems likely to serve a useful purpose as an introduction to the subject.

THE PRINCIPLES AND PRACTICE OF ENDOCRINE MEDICINE.

By William N. Berkeley *Lea and Febiger*

$4.50 6¼ x 9½; xi + 368 *Philadelphia*

While primarily intended for physicians in active practice this book will be found useful to the student of general biology

interested in any aspect of endocrine physiology. It reviews succinctly, impartially, and therefore somewhat uncritically, the extensive literature of this field. There are scattered through the book a good many interesting clinical observations by the author himself. It is well indexed.

BIOCHEMISTRY

APPLIED BIOCHEMISTRY

By Withrow Morse *W. B. Saunders Co.*
$7.00 $6\frac{3}{4}$ x $9\frac{3}{4}$; 958 pp. *Philadelphia*

This new and imposing text-book of biochemistry is written with the medical student directly in mind. The underlying philosophy is that if the medical curriculum is not to become overloaded and unbalanced each ancillary science must present only such material as is definitely related to medicine as a whole. Acting on this principle the author has made this a text-book of biochemistry as *applied* to medicine. It is both a laboratory manual and a didactic treatise. There are over 250 illustrations, many of them of apparatus. The wisdom of including so many cuts from apparatus dealers' catalogues seems doubtful. It is not unreasonable to suppose that a medical student already knows what an Erlenmeyer flask looks like. If he does not, he is certain to find out in the laboratory. Noteworthy features of the book are the great number of structural formulae given, and the series of portraits of living American biochemists. Since the book is intended strictly as a teaching manual, the final verdict as to its usefulness must rest with the experience of teachers. It has a detailed index.

CHEMICAL PATHOLOGY. (*Being a Discussion of General Pathology from the Standpoint of the Chemical Processes Involved.*)

By H. Gideon Wells *W. B. Saunders Co.*
$8.50 $6\frac{3}{4}$ x $9\frac{3}{4}$; 790 *Philadelphia*

In this fifth edition of the standard work on the chemical aspects of pathology the entire material has been worked over anew and the book rewritten. The size has been kept about the same as in the previous edition, largely by the expedient of dropping elementary material for which there is no longer need in such a book on account of the development of the teaching of biochemistry to medical students, and its replacement by new material marking recent developments of the subject. As a text-book for the medical student and a reference work for the general biologist, this work stands in the first rank.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *In 75 Vorlesungen. Für Studierende, Ärzte, Biologen und Chemiker. I Band: Organchemie. I Lieferung: Bausteine des Organismus—Blut. Vorlesung I Bis XVI.*

By Prof. Dr. Otto Fürth *F. C. W. Vogel*
15 marks *Leipzig*
7 x 10; xiii + 208 (paper)

This is a revised edition, brought up to date, of the author's well known lectures on the problems of physiological and pathological chemistry. Its appearance has been delayed by the War. In its revised form the book will consist of two volumes in six *Lieferungen*. This first *Lieferung* deals with the following subjects: Protoplasm and the characteristics of the proteins; Aliphatic elements of the protein molecule; Cyclic elements of

the protein molecule; Hydrolytic splitting; Oxidative degradation of protein; Albumoses and peptone; Polypeptids; Carbohydrates; The simple fats and phosphatides; Cholesterin; Nucleic acid; Blood clotting; Blood serum; Haemoglobin; Haematin and its derivatives; Lymph, exudates and transudates.

BRIGHTER BIOCHEMISTRY. *Being the Illustrated Journal of the Biochemical Laboratory, Cambridge. No. 3.*
By D. M. Needham, M. G. L. Perkins, M. D. Whetham.
The Sir William Dunn Institute
2s. 6d. *Cambridge, England*
6¼ x 10; 64 (paper)

This year's volume of Brighter Biochemistry is good fun, as usual. The fooling is always pointed and sometimes extremely clever. Paradoxically Brighter Biochemistry tends to arouse serious and somewhat uncomfortable reflections on this side of the water. The deadly and devastating seriousness with which the American graduate student, statistically speaking, naturally takes every aspect of his life and his work seems somehow more pitiful than ever with B. B. in one's hand. And the worst of it is that all too often the only slogan that he ever hears from his professors is that well-known and greatly over-rated one about life being real and earnest.

SEX

HYGIENE OF SEX.
By Max von Gruber
The Williams & Wilkins Co.
$1.50 5 x 7½; xii + 169 *Baltimore*

The topics discussed in the nine chapters of this book are as follows: Fertilization; Heredity and breeding; The organs of sex; The sexual instinct and the assumed necessity of coitus for health; The results of sexual excess and rules for the marital sexual intercourse; The limitation of conception; Aberrations of the sexual instinct; Venereal diseases and their prevention; Marriage or free love.

The real underlying philosophy of this treatise is indicated with entire fairness in the following quotations:

"Even the most sensual persons are not always sexually stimulated. Stimulation occurs only intermittently, as a rule only as a result of external influences, and it disappears spontaneously after a certain period if the external cause ceases to be operative" (p. 86).

"Manifestly, this discussion suggests that much can be done to prevent these stimuli. One can avoid drinking large amounts of fluid in the evening. One can take care to keep the bowels regulated. One may wear loose clothing and avoid the excessive pressure on the sexual organs by crossing the legs or by heavy bed clothes. One can prevent all unnecessary contact of the sexual organs with the hand. Washing and bathing will cleanse the skin. Medical care can be given early to skin eruptions, etc." (pp. 87–88).

"Mild disturbances and uncomfortable sensations, like restless sleep due to erection of the penis, and the frequent discharge of semen, headache and a conscious nervous tension can, as a rule, be easily avoided through the application or the methods previously mentioned. A moderation in eating, abstinence from alcoholic drinks and strongly seasoned food, a cool and not too soft bed, washing and bathing in cold water, and, particularly, an abundance of physical exercise, even to the point of fatigue, will be found to be definitely helpful. The con-

sistent avoidance of all those things which stimulate the sexual instinct renders abstinence the more readily accomplished, and, indeed, as we have already said, for this there is a physiological basis, since with lack of use of the sexual apparatus the testes curtail their activity" (pp. 93–94).

To complete the consideration of this antiquated, anaemic, academic, and asinine treatise, the following points seem relevant and worthy of record: (1) In 1925 the author was 72 years old; (2) 300,000 copies of the German edition were "sold abroad"; (3) *Ecce jam Europa!*

BIOMETRY

PELLIPLANIMÉTRIE. (*Mesure de la Surface du Corps Humain et Autres Corps.*)
By Dr. B. Roussy *Gaston Doin et Cie*
3 francs $5\frac{3}{8}$ x $8\frac{1}{2}$; 27 (paper) *Paris*

This pamphlet is a succinct résumé of the author's original contributions to the problem of the measurement of the surface area of the living body. All students of anthropometry and metabolism will find it stimulating and interesting.

PSYCHOLOGY AND BEHAVIOR

DWELLERS IN THE JUNGLE.
By Lieut.-Col. Gordon Casserly
Ward, Lock and Co., Ltd.
5 shillings $6\frac{1}{4}$ x $8\frac{1}{4}$; 255 *London*

These nature stories fall in manner somewhere between William Beebe and Rudyard Kipling. They are fascinatingly interesting and seem to be based upon extensive observation of animals in the Indian jungles. They deal respectively with a baby elephant, langur apes, the jungle fowl, wild dogs, a crocodile, the weaver bird, a pet monkey, and a female elephant. We commend the book highly to anyone who loves nature or has children.

TASTSINN, STRÖMUNGSSINN UND TEMPERATURSINN DER TIERE UND DIE DIESEN SINNEN ZUGEORDNETEN REAKTIONEN. (*Zoologische Bausteine, Band 1, Heft 1.*)
By Konrad Herter *Gebrüder Borntraeger*
G. M. 12 $6\frac{1}{2}$ x 10; iv + 182 *Berlin*

This book, the first in a new series, is a careful compilation of what is known about the reactions of lower animals to tactile, current (both air and water) and temperature stimuli. There is a bibliography of 343 titles and a detailed index. It will be a useful work of reference to all students of animal behavior.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

IS IT GOD'S WORD? (*An Exposition of the Fables and Mythology of the Bible and the Fallacies of Theology.*)
By Joseph Wheless *Wheless Publishers*
$4.00 *105 West 40th Street,*
$6\frac{1}{4}$ x $9\frac{1}{4}$; xxv + 475 *New York City*

The writer of this extraordinary book is a distinguished lawyer. His purpose is to present a detached, calm, and in fact truly scientific, analysis of the Bible as a whole.

"No man, priest, parson, or zealot for his inherited faith, can say with truth that this book 'attacks the Bible,' or seeks to defame the Bible God or to ridicule the Christian Religion. If such

results follow, the Bible itself is to blame, if this book of mine speaks truly. This book is based wholly on the Bible; its all but every reference and citation is to the texts of the Bible, faithfully quoted in exact words of inspiration. The Hebreo-Christian God is depicted in the plain words of revelation for his every word and deed attributed to him by the inspired writers. This book is simply the Bible taken as a whole, and thus viewed in a light not shed upon it by pulpit expoundings of golden texts or private casual readings of isolated choice fragments.

"If the Bible and its derived dogmas suffer from this simple process of 'searching the Scriptures whether these things were so,' the fault, dear reader, is not in the candid writer of this book, but in The Book, which utters the things which are simply and truly quoted and compared, in simple juxtaposition of contradictory texts, and not in the usual isolated and scattered passages as is the custom of sermons and pious tracts. Here is my book; there lies the open Bible; any man who will read, and is curious or interested for the truth, may judge wherein is the truth" (pp. xxiii–xxiv).

The results of this simple and novel procedure, which is carried out with good judgment, a modicum of humor, and an entire absence of rancor, may fairly be called stupendous. We commend the book in the strongest terms to our readers because we believe that probably few of them have any *adequate* conception of just what kind of a book the Bible really is. A more effective answer to fundamentalism than Mr. Wheless' treatise is inconceivable.

We are informed that the publication of this important book has been taken over by Alfred A. Knopf, Inc.

LANDMARKS IN THE STRUGGLE BETWEEN SCIENCE AND RELIGION.
By James Y. Simpson *George H. Doran Co.*
$2.00 5½ x 8; xv + 288 *New York*

J. W. Draper's *The Conflict between Religion and Science*, and Andrew D. White's *A History of the Warfare of Science with Theology in Christendom*, are the classic works in the field they cover. Neither has ever been successfully controverted in respect either of its main facts or conclusions. The present book covers essentially the same ground, but its attitude leans much more sympathetically towards the religious side of the controversy than is the case with either of its predecessors. Mr. Simpson's egg was boiled a very much shorter time than either Mr. Draper's or Mr. White's.

MATTER, MAN AND MIND.
By W. F. F. Shearcroft *The Macmillan Co.*
$3.00 5¾ x 8¾; 191 *New York*

This entertaining and well-written volume wanders widely over the whole range of science, but with a great deal more emphasis upon biological than upon physical matters. It ought to have a wide popular appeal. Its science is sound, its style has clarity and real charm, and it avoids the blatancy of the yellow journal, which in America is rapidly coming to be regarded as the highest ideal of popular scientific writing.

RELIGION AND NATURAL SCIENCE.
By E. Haigh *Student Christian Movement*
4s. 6d. 5¼ x 8; xi + 170 *London*

This is a religious tract written by a secondary school teacher of physical science. Its obvious purpose is to keep

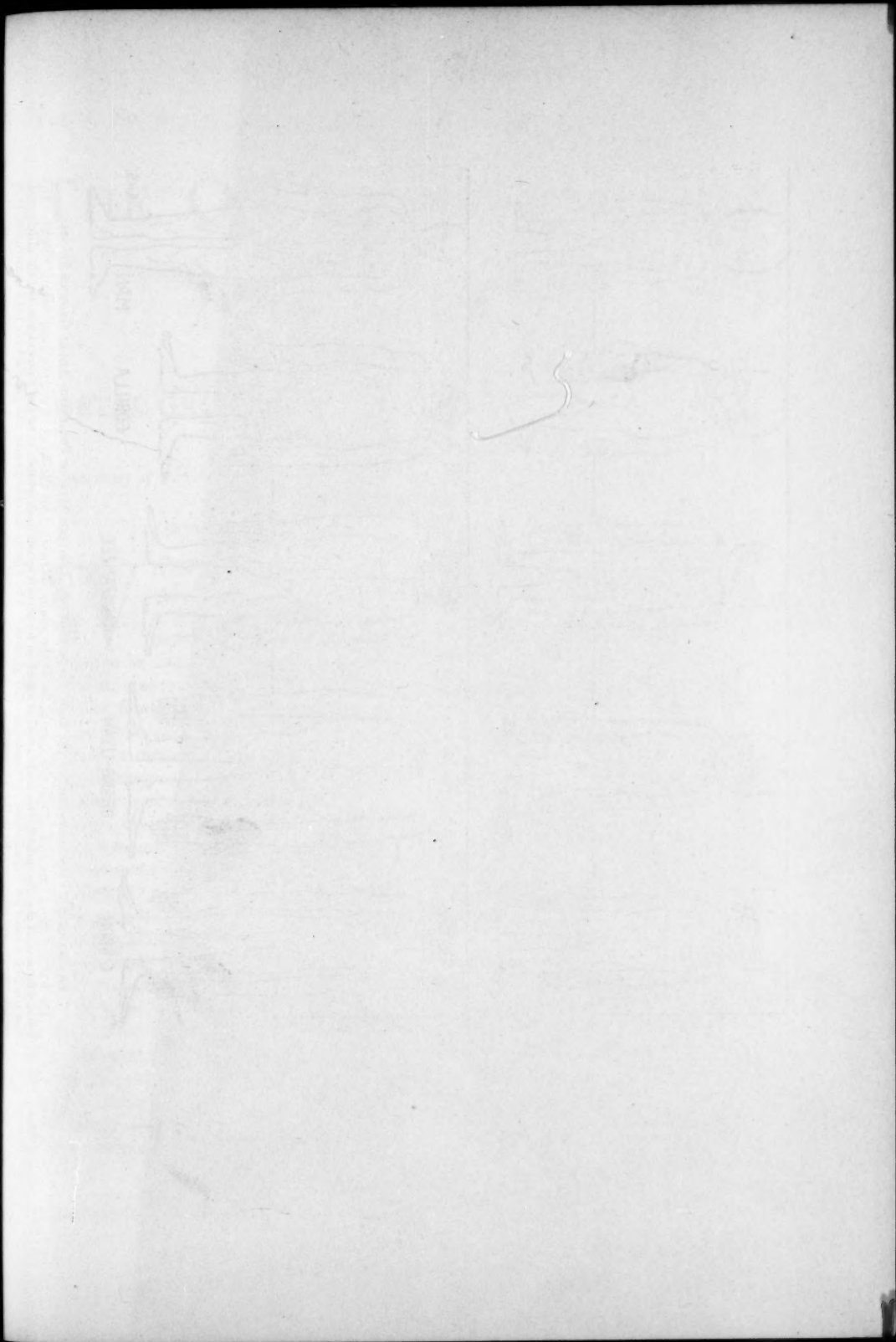
bright young boys and girls, who may chance to become interested in science, from straying out of the safe and pleasant fold watched over by the pastor. We are told that "Faith is not a weaker kind of knowledge, a sort of crutch to lean upon when our footing is not secure. It is the exercise of a higher faculty than the intellect" (p. 117).

HOMÖOPATHIE. *Kritische Gänge Hüben und Drüben. (Moderne Biologie Heft 10.)*
By Prof. Dr. Hans Much *Curt Kabitzsch*
4.20 marks 5 x 7½; 142 *Leipzig*

A welcome candidate to the Budget of Biological Paradoxes. It is a quasi-philosophical discussion of what homeopathy is, what it is not, and what it should be in the light of modern biological knowledge.

DISEASE PREVENTION.
By Herbert H. Waite *Thomas Y. Crowell Co.*
$4.50 6 x 9; xi + 667 *New York*

This treatise on preventive medicine strictly follows the conventional lines. Its interest would have been enhanced by illustrations and by greater conciseness. Its chief usefulness seems likely to be as a convenient reference work.

THE AMERICAN ILLUSTRATED MEDICAL DICTIONARY. *(A New and Complete Dictionary of the Terms Used in Medicine, Surgery, Dentistry, Pharmacy, Chemistry, Nursing, Veterinary Science, Biology, Medical Biography, etc., with the Pronunciation, Derivation, and Definition, Including much Collateral Information of an Encyclopedic Character.)*
By W. A. Newman Dorland
W. B. Saunders Co.
$7.00 6½ x 9; 1344 *Philadelphia*

The thirteenth revised and enlarged edition of this well-known and thoroughly established medical dictionary contains about 2500 new words. Dorland's Dictionary is a never failing resource to the biologist who finds himself entangled in the intricacies of medical technicalities.